POPULATION AND REPRODUCTIVE ECOLOGY OF *TURBO SMARAGDUS* IN THE KAIKOURA REGION.

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ABSTRACT

Turbo smaragdus is a herbivorous gastropod of the intertidal and sub-littoral zones, which is distributed widely along the coastline of New Zealand. This study sought to investigate the population and reproductive ecology of *Turbo* on the Kaikoura Peninsula. This involved the determination of: spatial and temporal distribution patterns, associations with other herbivorous molluscs and algal species, recruitment of juveniles, morphometric relationships, population length-frequency structures, growth rates, spawning seasons, trends exhibited in a reproductive cycle, sex ratio, size at sexual maturation and fecundity.

Turbo have a broad distribution that varies significantly both within and between sites. Transect surveys determined that *Turbo* have an aggregated distribution, and were present from the upper eulittoral into the sub-littoral to depths of 3m with largest numbers generally occurring in the mid-eulittoral. Juveniles (shell lengths $\leq$ 15mm) occurred widely on the vertical profiles of the shores sampled, but larger individuals were more common in the lower eulittoral. Sub-littoral populations were composed of larger individuals, with shell lengths $\geq$ 35mm.

As *Turbo* grow, shell and operculum height, width and length increase linearly and shell, operculum, body tissue and gonad weight exponentially.

Tag-recapture data indicate that growth rates decrease with increasing size of individuals. At the sites sampled, individuals can grow to a shell length of 40mm at which the von Bertalanffy growth curve predicts they will be approximately ten years of age. Growth rates of *Turbo* vary seasonally, with greatest rates occurring between November-March, and the slowest between August-November. Spatial variation was also shown to occur between two populations, with greater growth rates occurring in the area of slightly greater exposure to wave action. The absence of age classes in length-frequency histograms suggests that recruitment failure or high mortality rates may occur during some years.

Sexual maturation of both male and female *Turbo* generally occurred between shell lengths of 20-25mm, although a few individuals were observed to mature at both smaller and larger sizes. Energetic investment in reproductive effort, which is indicated by increasing gonad size and fecundity, increases with increasing shell lengths. The populations sampled exhibited a 1:1 sex ratio.

Turbo are broadcast spawners and have a distinct annual reproductive cycle. A major spawning event occurred on the Kaikoura Peninsula during February-March 1991 and a minor event in January 1992. Immediately succeeding the 1991 spawning period, the gonads of both sexes were reduced in volume and relatively depleted of mature gametes. Gametogenesis occurred within several months of spawning, with the immature gametes developing slowly throughout the winter and accelerating in growth in the spring to produce gonads that were densely packed with mature gametes several months prior to the January 1992 spawning event.

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GENERAL INTRODUCTION

1.1 INTRODUCTION

1.1.1 Background

Early marine ecological studies were generally qualitative, focusing on broad descriptions of the abundance and distribution of organisms in the intertidal (Stephenson and Stephenson 1949, Knox 1953, Morton and Chapman 1968, Morton and Miller 1968). In later studies, specific sampling techniques (eg. Andrew and Mapstone 1987), were developed to quantify qualitative observations and determine the factors that influenced the distribution of the organisms on the shore. Such studies investigated biotic interactions including intra-specific (Fletcher and Creese 1985) inter-specific (Creese and Underwood 1982), predator/prey (Luckens 1966) and herbivore/algal relationships (Underwood and Jernakoff 1981, Steneck and Watling 1982). It is from both qualitative and quantitative observations of the shore that models predicting the occurrence of organisms are derived (eg. Underwood and Denley 1984). It is generally accepted that the community structure of the shore is complex and varied, with zonation of the shore attributable to the interaction of both physical and biotic factors.

More recently, there has been increasing emphasis on the management of specific species for commercial and conservational values. For example, the New Zealand Quota Management System (Annala 1989). If effective management of a species is to be achieved, an understanding of specific population parameters and dynamics is required. This includes a working understanding of not only the abundance and spatial distribution of the population, but also size, sex and age distributions, movement, mortality, recruitment, and modes of reproduction; and reproductive cycles.

1.1.2 Study Animal

Turbo smaragdus is a generalist grazing gastropod of the intertidal zone. Closely associated with the trochids, *Turbo* is a member of the Turbinid family,[1] whose distinguishing characteristic is a hard calcareous operculum **(Figure 1.1)**. It is from the distinctive green and white colouration of the operculum that the common name, Cats Eye, is derived.

Figure 1.1 Adult and juvenile *Turbo* amongst coralline turf as viewed during low tide at Avoca Point, Kaikoura Peninsula. The green and white calcareous operculum which characterises *Turbo* is shown on an upturned individual (centre).

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[1] *Turbo granosa* is another species of the *Turbo* genus which occurs in New Zealand. For further information pertaining to the classification of *Turbo smaragdus* and other New Zealand species of the Turbinidae family and *Turbo* genus, please refer to Appendix I.

Turbo are widely distributed along the coastline of New Zealand, extending from the upper littoral to the sublittoral zones of the shore. They occur on a wide range of substrata, from hard to soft, in areas varying from extremely sheltered to those of considerable exposure (Morton and Miller 1968).

Most studies investigating the ecology of *Turbo* have been done in the Auckland region. The distribution and abundance of *Turbo* was initially investigated by Smith (1969). Walsby (1977) related the distribution of *Turbo* on the shore to growth and movement. The relationship between movement and feeding ecology was examined by Beckett (1969). Edwards (1982) investigated feeding ecology and the interactions of *Turbo* with other dominant grazers of the intertidal. Breeding cycles were examined by Grange (1974) who determined spawning seasons, stimulus and larval development.

In the Kaikoura region, *Turbo* has been included in descriptions of the intertidal ecology of the Kaikoura Peninsula (Rasmussen 1965, Marsden 1981).

Although *Turbo* are at present not commercially fished, interest has been exhibited in the commercial harvest of the species for the operculum to be used as jewellery and the meat to be canned and marketed as a delicacy.

1.1.3 Objectives

The broad objective of this study was to determine the population and reproductive ecology of *Turbo* in the Kaikoura region. This was achieved by the establishment and subsequent investigation of specific population and reproductive parameters such as:

a) Distribution. This involved:

- Determination of the size distribution of *Turbo* in the intertidal, and how it varied through time (temporally) and between sites (spatially).
- Estimation of the recruitment of juvenile *Turbo* into the adult population.
- Establishing the associations of *Turbo* with other herbivorous molluscs and macro-algae of the intertidal, and to a lesser extent, those of the sublittoral.
- Exploratory investigation of the density and size distribution of sublittoral *Turbo* populations at one site.

b) Morphological Relationships.

- Shell, operculum and body dimensions were measured and related to each other to determine how these parameters vary as *Turbo* increase in size.

c) Growth. This involved:

- Sampling of *Turbo* populations to determine population length/frequency structures.
- Tag-release of individuals to estimate seasonal and annual growth rates and determine if they varied between sites.
- Estimation of age at size for two populations using a von Bertalanffy growth model.

d) Reproduction. This involved:

- Determination of spawning events.
- Descriptions of gametes and gametic activity throughout a reproductive cycle for both male and female *Turbo* by way of histological examination.
- Estimation of fecundity of females, sex ratio and size at sexual maturation.

1.2 STUDY AREA

1.2.1 Kaikoura Peninsula

The Kaikoura Peninsula is situated on the east coast of the South Island, New Zealand, **(Figure 1.2)**, positioned towards the northern margins of a subtropical convergence. Local ocean waters are derived from the south flowing East Cape Current with influxes of sub-antarctic water from the Canterbury Current. (Garner 1961). Southerly seas prevail in winter and north-easterlies in summer (Rasmussen 1965).

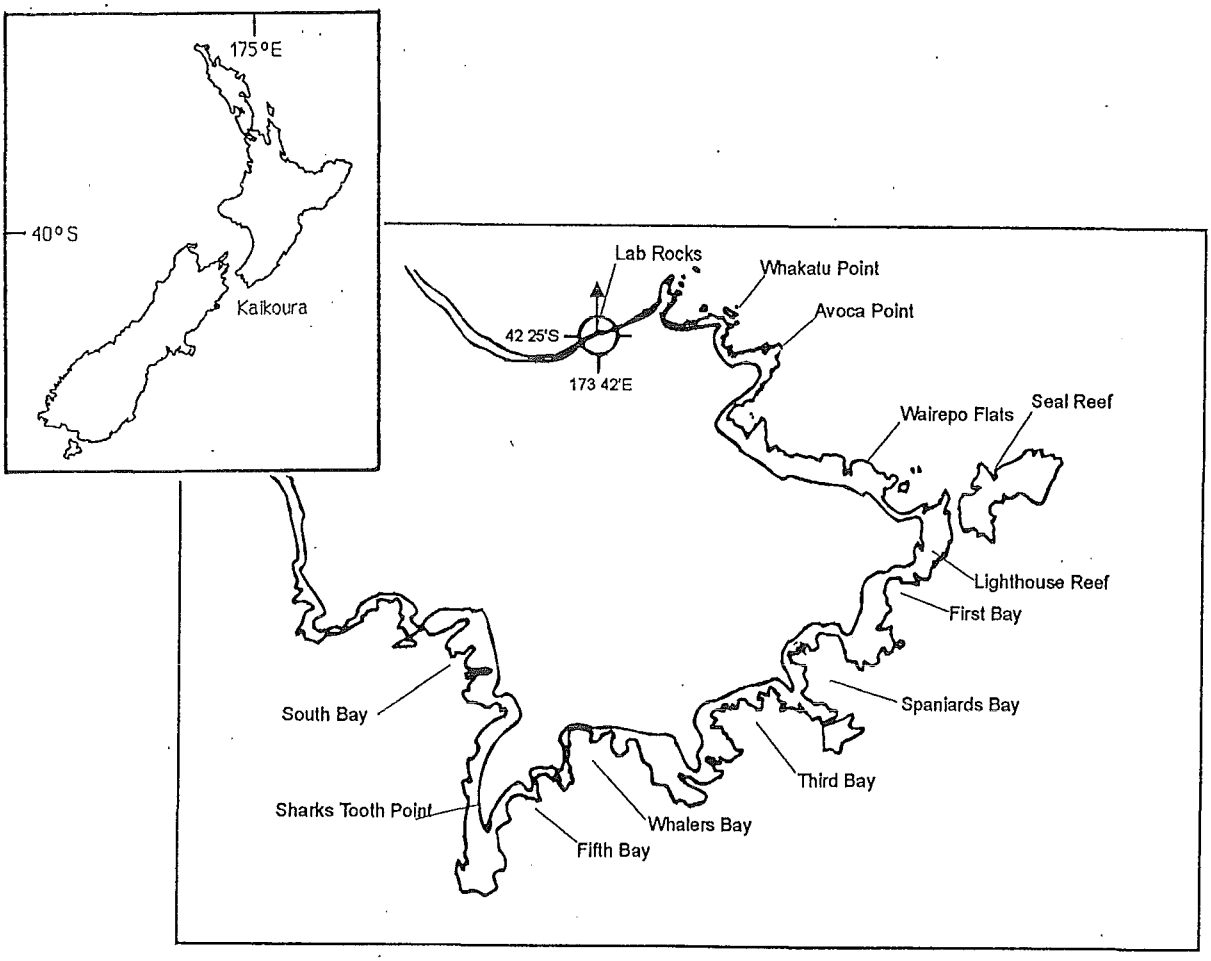


Figure 1.2 Location of the study area in New Zealand and map of the Kaikoura Peninsula.

A narrow isthmus extending 4.5 kilometres seaward, the Peninsula itself is a hilly plateau which abruptly drops approximately eighty metres to the gently sloping platforms of the intertidal. Of sedimentary origin, the platforms alternate between bands of convoluted limestone and smoother siltstone (Rasmussen 1965). These vary in width, though in places extend one hundred metres seaward where, at the approximate margin of the sublittoral, they drop to the seafloor (Marsden 1981). Other shores of the Peninsula are comprised of gravel, sand, limestone and intertidal boulder fields (Rasmussen 1965).

1.2.2 Specific Study Sites

Five specific areas on the Kaikoura Peninsula were selected as study sites for different components of this study. These include:

Spaniards Bay (Figure 1.3). Situated on the south east face of the Peninsula, this bay is semi-enclosed by two limestone platforms that project seaward. Limestone shingle has accumulated above and between the platforms to form a steep beach.

Avoca Point (Figure 1.4). A gently sloping platform of argilleous siltstone situated on the northern face of the Peninsula. A north-easterly aspect ensues exposure to easterly and northerly seas.

Whakatu Point (Figure 1.5). A projection of low lying, highly convoluted, ridged limestone situated on the northern face of the Peninsula. Similar aspect and exposure to seas and winds as described for Avoca Point.

Lighthouse Reef (Figure 1.6). A broad, gently sloping siltstone shelf situated on the southern face of the Peninsula. A south-easterly aspect allows exposure to both easterly and southerly conditions.

Lab Rocks (Figure 1.7). A low lying shore composed predominantly of limestone boulder and rubble interspersed with fine sediment flats. Situated directly in front of the Edward Percival Field Station on the northern face of the Peninsula, this site is sheltered from southerly conditions but exposed to north-eastern.

Other sites dicussed in this study include:

Paia Point. A small projection of the coast 15.5km south of the Kaikoura Peninsula, exposed to both southern and northern seas. A steep, shingle beach at the top of the shore slopes down to greywacke boulders and cobbles.

Haumuri Bluffs. These are limestone cliffs situated 21km south of the Kaikoura Peninsula. The northern side is sheltered from southerly seas and exposed to the north-easterly seas of summer, while the southern side is exposed to southerly conditions.

Figure 1.3 Spaniards Bay, Kaikoura Peninsula.

Figure 1.4 Avoca Point, Kaikoura Peninsula.

Figure 1.5 Whakatu Point, Kaikoura Peninsula.

Figure 1.6 Lighthouse Reef, Kaikoura Peninsula.

Figure 1.7 Lab Rocks, Kaikoura Peninsula.

CHAPTER TWO

PATTERNS OF DISTRIBUTION AND ASSOCIATIONS

2.1 INTRODUCTION

The distribution of a species can be described in terms of: **a)** the broad-scale, spatial occurrence of populations, **b)** the spatial occurrence of individuals within those populations, and **c)** how these spatial distributions change throughout time (temporally).

These distributions are influenced by the interaction of factors such as reproductive and life history strategies, external conditions such as currents, physiological and morphological constraints, inter and intra-specific competitive interactions, locomotory ability, nutritional requirements and feeding modes (Underwood 1979). As a consequence, considerable spatial and temporal variation can occur on both large and small scales. A description of a species distribution is therefore fundamental to the description and understanding of its ecology.

Turbo smaragdus is widely distributed along the shores of New Zealand's North and South Islands (Morton and Miller 1968) and is a dominant grazer of the mid and low eulittoral of Echinoderm Reef at Leigh (Smith, 1969, Walsby 1977, Edwards 1982) and the Kaikoura Peninsula (Rasmussen 1965, Marsden 1981). At Leigh, the upper limit of *Turbo's* intertidal distribution overlaps with that of *Melagraphia aethiops* (Walsby 1977) and its lower limit overlap with that of the limpet, *Cellana radians* (Edwards 1982). Larger *Turbo* occur in the sub-littoral zones of the Kaikoura Peninsula (Rasmussen 1965), and in the Auckland region (Beckett 1969). Densities of *Turbo* vary considerably between and within sites (Marsden 1981), with shell size correlating to shore height at some northern New Zealand sites (Grange 1974, Walsby 1977).

This study sought to examine: **1)** spatial and temporal size-class distribution of *Turbo* within and between sites, **2)** associations of *Turbo* with particular substratum types, **3)** associations of *Turbo* with flora and other molluscs of the shore, **4)** recruitment of juvenile *Turbo* within and between sites, **5)** occurrence of sub-littoral populations of *Turbo*.

2.2 MATERIALS AND METHODS

2.2.1 Spatial Sampling

Three sampling methods were used to evaluate the spatial distribution and associations of *Turbo* on the Kaikoura Peninsula.

a) Intertidal densities and associations.

In January 1991, the densities and associations of *Turbo* with respect to other herbivorous molluscs, algal species and substratum types of the intertidal shore were sampled using strip-transect techniques at Spaniards Bay and Whakatu Point **(Figure 1.2)**. Three transects, parallel and separated by approximately 50m, were sampled at both sites. Transects were continuous strips 5 metres wide that extended from the upper-littoral to the edge of the sub-littoral zone and were divided into 10m sections. Each 5x10m section was randomly sampled 5 times using a 0.25m^2 quadrat. Within each quadrat;

-Numbers of *Turbo, Melagraphia aethiops, Diloma* species, Limpet species (acmeid and patellid), *siphonaria* species, chiton species, and littorinid species were counted.

-Percentage cover of algal species such as *Hormosira banksii, Corallina* species, small and large brown algal species, small greens, filamentous reds, foliated reds was estimated.

-Percentage cover of each substratum type and rock pools was estimated. Substratum types were categorised as consolidated (silt/limestone rock) and unconsolidated (mud, sand, gravel). Rock pools were defined as depressions in the substratum that contained water with a depth >2cm.

To estimate percentage cover of algal species and substrata types, the quadrat was divided into nine squares with string. Each section comprised 11.1% of the entire quadrat. The proportion of each algal species or substratum type that occurred within each square was used to estimate the overall % cover (for each category) for the entire quadrat.

Each transect was surveyed using a theodolite to determine shore heights and shore profiles were drawn.

The mean densities of herbivore species and percentage cover of algal species which occurred most frequently on the shores were plotted with standard errors for each 5x10m section of transect and superimposed onto shore profiles. Association data were statistically interpreted using a correlation matrix.

b) Intertidal abundance and length/frequency distributions.

In January 1992, the abundance and length/frequency distributions of *Turbo* were determined at Spaniards Bay, Whakatu Point and Lighthouse Reef, using strip transect techniques. Three transects were sampled per site, each sampled as described above (section 2.2.1b), except that each 5x10m section of transect was randomly sampled 10 times using a 0.25^2 quadrat. Within each quadrat, numbers of *Turbo* were counted and shell lengths recorded within 5mm (shell length) categories. Each transect was surveyed using a theodolite to determine shore heights and shore profiles were drawn.

To illustrate smaller scale distribution patterns of *Turbo* on the shore, the number of quadrats were plotted against number of *Turbo* per quadrat. Length/frequency histograms of *Turbo* were plotted for each 5x10m section of each transect and superimposed onto shore profile plots. The mean number of *Turbo* which occurred in the lower, middle and upper 5x10m sections of each transect were used to test statistically for spatial variation in numbers of *Turbo*. Raw data was log transformed, and tested using Cochran's Test (Winer 1962) and Analysis of Variance (ANOVA) (Sokal and Rohlf 1981).

c) Sub-littoral densities and associations.

The three transects sampled in the intertidal at Spaniards Bay in January 1991 were extended into the sub-littoral. Sub-littoral transects were continuous strips 5x40m in length and divided into 10m sections. Each 5x10m section was randomly sampled using a 0.25m^2 quadrat. In each quadrat, the numbers of *Turbo* were counted and shell lengths measured to the nearest 5mm, percentage substratum type and algal cover were estimated (as described above, section 2.2.1a) and occurrence of other herbivorous molluscs noted. Seafloor height below Mean Sea Level were estimated by adjusting readings from a depth gauge for tidal variations.

Mean densities of *Turbo*, percentage cover of algae species and substratum category were graphed with standard errors for each 5x10m section of transect and superimposed onto seafloor profiles.

2.2.2 Temporal Sampling.

Two transects, one at Spaniards Bay and the other at Avoca Point, were sampled at monthly intervals between April 1991-March 1992. Transects were divided into three shore heights of high, mid and low, each with an area of 10x10m, by attaching permanent tags to the substratum (Spaniards Bay: high = 0.03m, mid = -0.21m and low = -0.32m; Avoca Point: high = 0.31m, mid = -0.08m, and low = 0.10m)[1].Each shore height was randomly sampled 10 times using a 0.25m^2 quadrat. In each quadrat numbers of *Turbo* were counted and shell lengths measured to the nearest 5mm. Transects were surveyed with a theodolite to determine shore heights and shore profiles plotted.

[1] The tidal heights of each shore were measured relative to the Lyttleton Tide Gauge Mean Sea (M.S.) Level.

Monthly length/frequency histograms of *Turbo* within each shore height were plotted for Spaniards Bay and Whakatu Point to show length/frequency distributions - throughout one year of sampling.

2.2.3 Recruitment

A pilot study was conducted on the 20-21 April 1992 as a precursor to a more extensive evaluation of the recruitment of *Turbo* on the Kaikoura Peninsula. Three sites at which juvenile *Turbo* (shell lengths 5-15mm) commonly occurred were selected (Avoca Point, Wairepo Flats and Seal Reef). Initially, two patches of coralline turf (50x50mm) from the mid-region of the shores were removed using a flat-bladed knife. The turf was examined for juvenile *Turbo* (shell length <<5mm) with a stereo microscope at 60x magnification. Several days later, a further two patches (100x100mm) were removed from the mid-shore level at Avoca Point and examined as described above. As a consequence of the results from this preliminary study, further turf patches were not examined to investigate recruitment.

Mid-shore regions were chosen for the more detailed investigation of the distribution of recruits because highest frequencies of *Turbo* 0-5mm in shell length occurred here during spatial and temporal sampling. Coralline turf was selected as the substratum to be searched for recruits because **a)** Walsby (1977) concluded that at Echinoderm Reef at Leigh, only those settlers which find shelter in coralline turf or crevices survive, and **b)** the larvae of other intertidal organisms such as; tubeworms, chitons and *Haliotis* larvae (Morse and Morse 1984) are known to recruit into crustose red algae.

2.3 RESULTS

2.3.1 Spatial Distribution.

The spatial distribution of *Turbo* on the Kaikoura Peninsula can be described in terms of:

a) Small-scale patterns of distribution in the intertidal.
b) Vertical distributions of length/frequency and abundance in the intertidal.
c) Occurrence and densities between sites.
d) Intertidal associations with herbivorous molluscs, algal species and substratum types.
e) Sub-littoral abundance and associations with herbivorous molluscs, algal species and substratum types.

a) Small-scale patterns of distribution in the intertidal.

Turbo exhibited a negative binomial distribution at the three sites sampled on the Kaikoura Peninsula **(Figure 2.1)**. The number of *Turbo* that occurred in any one quadrat at the three sites sampled varied between 0-50+. The highest frequency of quadrats had no *Turbo*, with quadrat frequency declining with increasing numbers of *Turbo*. For example, at Spaniards Bay, 134 quadrats had no *Turbo*, 17 quadrats had 4 *Turbo*, and 1 quadrat had 28 *Turbo*.

The maximum density of *Turbo* (77 per 0.25m^2) occurred at, Whakatu Point. However, *Turbo* did occur at greater densities than this. For example, 170 *Turbo* per 0.25m^2 were encountered during temporal sampling at Avoca Point. These results indicate that *Turbo* generally have an aggregated distribution that varies in number from several individuals to ≥170.

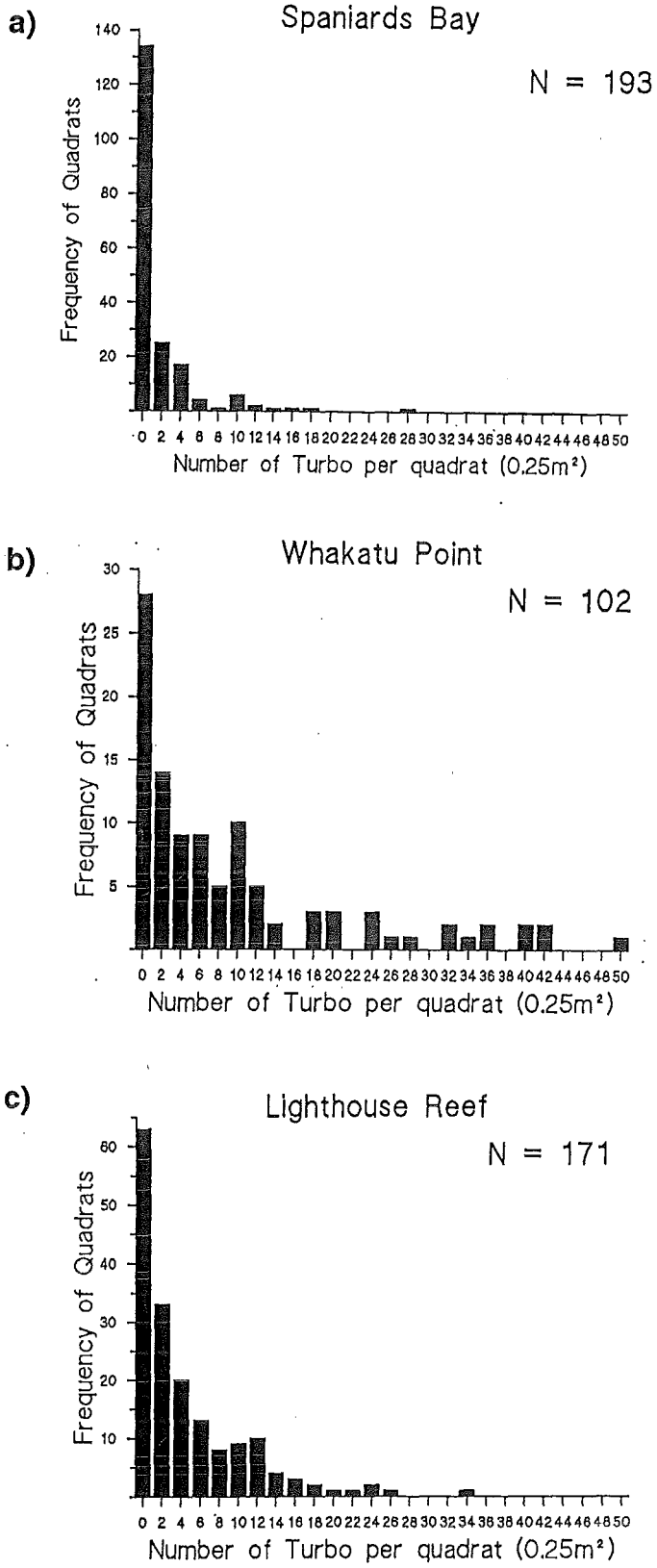


Figure 2.1 Frequency of quadrats against numbers of *Turbo* per quadrat (0.25m^2) at: **a)** Spaniards Bay, **b)** Whakatu Point, and **c)** Lighthouse Reef.

b) Vertical distributions of length/frequency and abundance in the intertidal.

In general, *Turbo* of smaller shell lengths were distributed throughout the intertidal zone, while larger individuals were restricted to the lower shore and upper margins of the sub-littoral zone. For example, along transect C at Whakatu Point **(Figure 2.2a)**[2] smaller *Turbo* (shell lengths 5-15mm) occurred at all tidal heights (0.33m to -0.12m), although at higher frequencies in the mid-shore region, while larger individuals (shell lengths ≥20mm) were present only at the upper margin of the sub-littoral (tidal height = 0.02m). However, this distribution pattern varied between transects and sites. For example, along transect B at Spaniards Bay **(Figure 2.2b)**, *Turbo* of shell lengths 20-25mm occurred at all tidal heights, with the exception of the highest (tidal height = 1.38).

[2] The length/frequency distributions of *Turbo* along the vertical profiles for the shores sampled, but not discussed in section 2.3.1b, are presented in Appendix II.

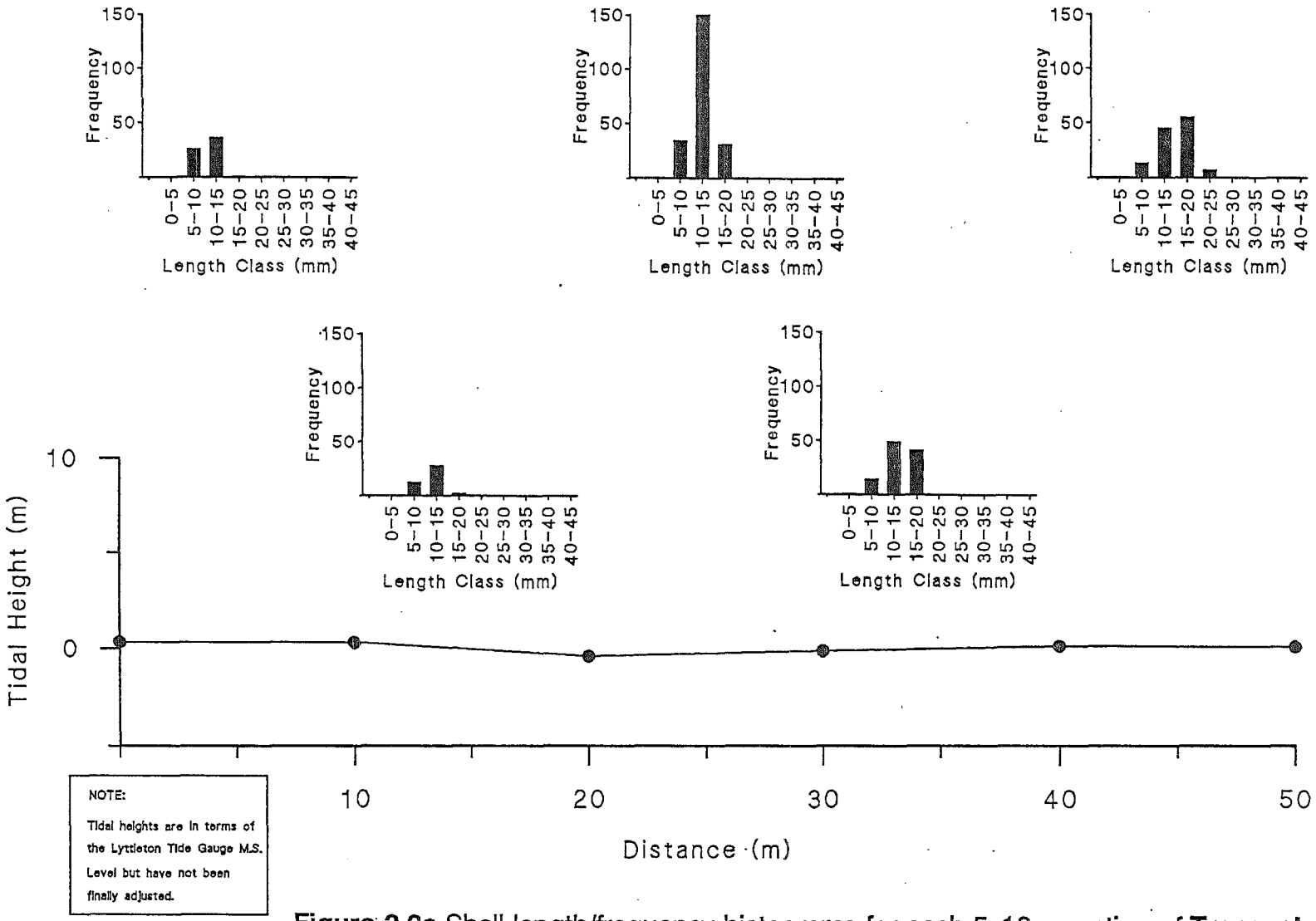


Figure 2.2a Shell length/frequency histograms for each 5x10m section of **Transect C** in the **intertidal, Whakatu Point.**

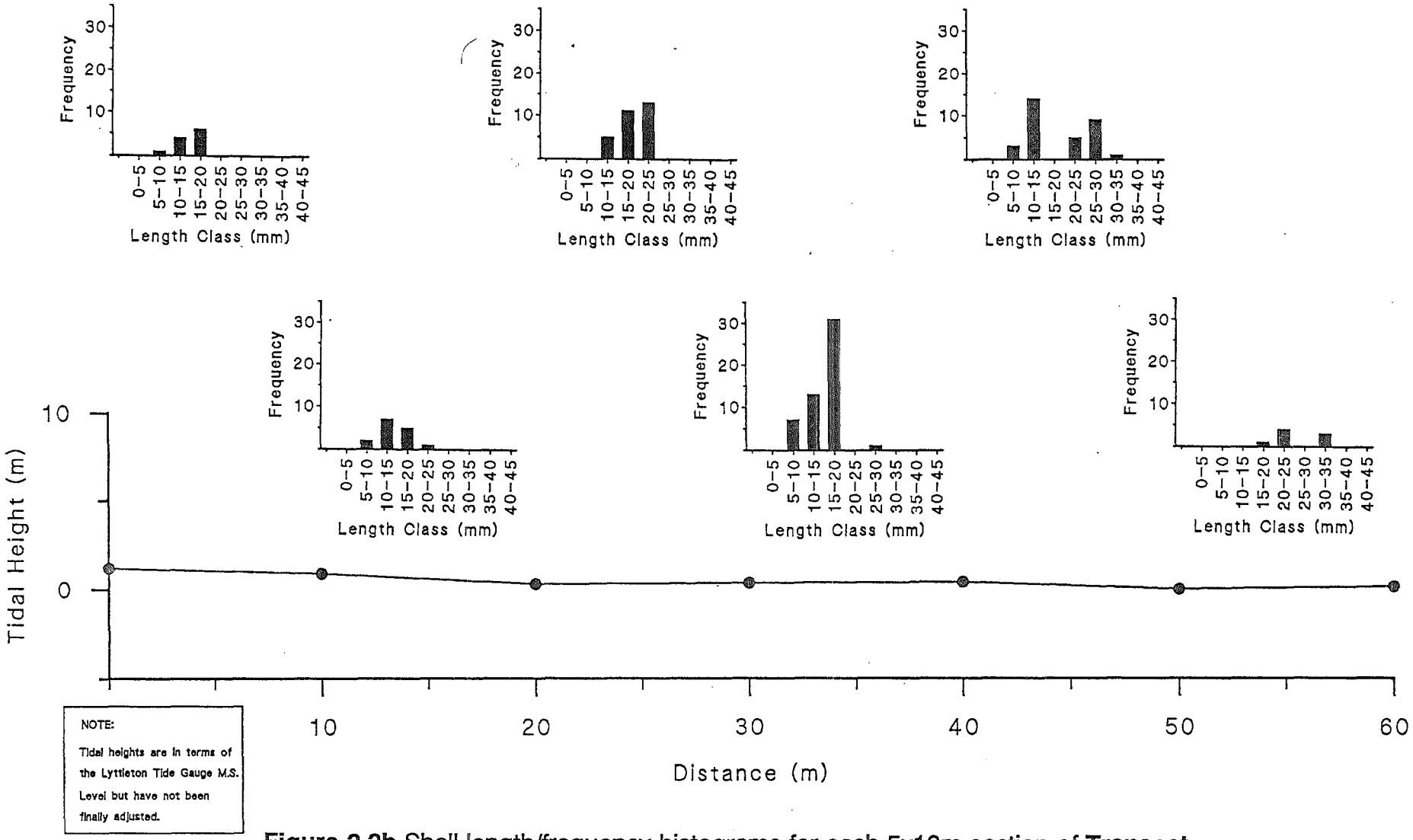


Figure 2.2b Shell length/frequency histograms for each 5x10m section of **Transect B** in the **intertidal, Spaniards Bay.**

Means, as derived by ANOVA (see below), indicate that mid-shore heights generally have greater numbers of *Turbo* than high or low shore heights **(Figure 2.3)**. For example, in January 1992, at Whakatu Point, the mean number of *Turbo* at high shore heights was 3.1, which increased to 10.9 at mid-shore levels, and 5.8 at low shore heights. However, exceptions do occur, for example at Spaniards Bay, where the highest numbers of *Turbo* occur at the lowest shore levels.

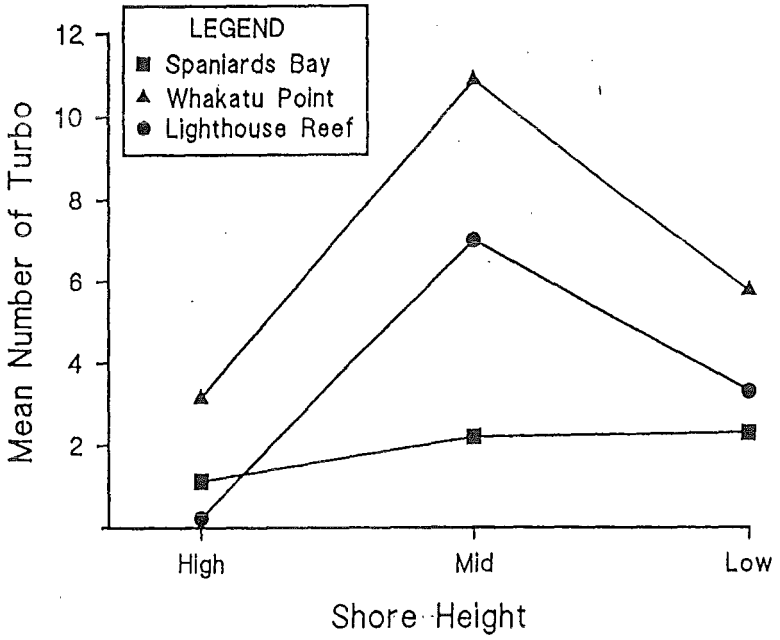


Figure 2.3 Mean number of *Turbo* at high, mid and low shore heights for three sites on the Kaikoura Peninsula. (Interaction terms).

c) Occurrence and densities of *Turbo* between sites.

Turbo in the Kaikoura Region occur widely over the intertidal zone, and at sites varying in substrata type. Turbo were present on: **a)** the limestone shores of Whakatu Point and Spaniards Bay, **b)** the argilleous siltstone of Lighthouse Reef and, although not sampled, **c)** the greywacke shores of Paia Point.

Variation occurred at all levels **(Table 2.1).** As expected, there was significant variation at the finer scales sampled (shore heights * transects within sites). There was a large residual, indicating that most of the variation in the numbers remains unexplained by the factors in the model.

Table 2.1 ANOVA analysis results of numbers of *Turbo* with sites, transects and shore heights. Raw data; Cochran's: ($C_{.99}$ (27,9) = 0.0084).

SOURCE	DF	SS	MS	F	P
Sites	2	16.71	8.36	10.11	0.000
Transect within Sites	6	32.08	5.35	6.47	0.000
Shore Height	2	32.87	16.44	19.89	0.000
Sites * Shore Height	4	9.06	2.27	2.74	0.029
Shore Hgt * Trans within Sites	12	27.78	2.31	2.80	0.001
Error	243	200.83	0.83		
Total	269	319.35			

d) Intertidal associations.

A data description from SAS of overall mean numbers and standard deviations (per 0.25m^2) of herbivorous molluscs and algal species **(Table 2.2)**, indicates that *Turbo* and *Melagraphia aethiops* are the most numerous grazers on the shores sampled.

Table 2.2 Mean percentage cover of substratum type and numbers (per 0.25m^2) of herbivorous molluscs and algal species at Avoca Point[3].

	CONSOL	UNCONL	POOL	TURB	MELG	LIMP	CHIT
MEAN	60.17	34.33	17.06	2.72	2.20	0.73	0.46
STD DEV	38.01	36.16	28.99	9.55	3.87	1.86	1.76
	HORM	CORL	CYST	RED	RALP	SMBR	GREN
MEAN	10.26	13.86	1.43	0.51	3.89	1.92	0.94
STD DEV	16.77	23.83	4.81	2.36	12.56	6.59	5.15

[3] CONSOL = consolidated substratum (eg. rock), UNCONL = Unconsolidated substratum (eg. mud, sand, gravel), POOL = rock pool, TURB = *Turbo smaragdus*, MELG = *Melagraphia aethiops*, LIMP = limpet species, CHIT = chiton species, HORM = *Hormosira banksii*, CORL = *Corallina* sp., RED = foliated & filamentous red algae species, RALP = *Ralphsia verrucosa*, SMBR = small brown algae, GREN = green algae.

The major herbivorous molluscs and algal species of the shores sampled included: *Turbo*, *Melagraphia*, Chiton sp., Limpet sp., *Hormosira*, and *Corallina* sp. These species were generally widely distributed over the shores sampled[4]. For example, although *Melagraphia* were generally more abundant in the mid-regions of the shores, this species occurred in both the upper and lower regions of shore, (e.g. transect B, Spaniards Bay) **(Figure 2.4a)**.

Strong trends in the association of *Turbo* with particular species[5] of the major herbivores and algal are not evident in graphical presentations of the association data for January 1992. For example, *Turbo* occur at low densities widely over the shore at transect B, Spaniards Bay (with the exception of the 0-10m section), despite the fluctuations of other species such as *Melagraphia*, *Hormosira* and *Corallina* sp..

The vertical distribution of *Turbo* on the shore generally overlapped with that of the second most common intertidal herbivore, *Melagraphia aethiops*. For example, both *Turbo* and *Melagraphia* are present, although at varying densities, at all shore heights in transect C, Whakatu Point **(Figure 2.4b)**. Diversity and abundance of algal species increases in the lower eulittoral and sub-littoral margins. For example, the majority of the small brown algal species listed in Appendix III were present in the lower shore regions of transect C, Whakatu Point, whereas at mid-shore levels, the dominant algal species were *Hormosira banksii* and *Corallina* sp., with some *Adenocystis* and *Colpomenia*.

[4] Graphical representations of the distribution of herbivorous molluscs and algal species not discussed in section 2.3.1.d are presented in Appendix IV.

[5] Please refer to Appendix III for a listing of molluscan and algal species that were encountered during spatial and temporal sampling.

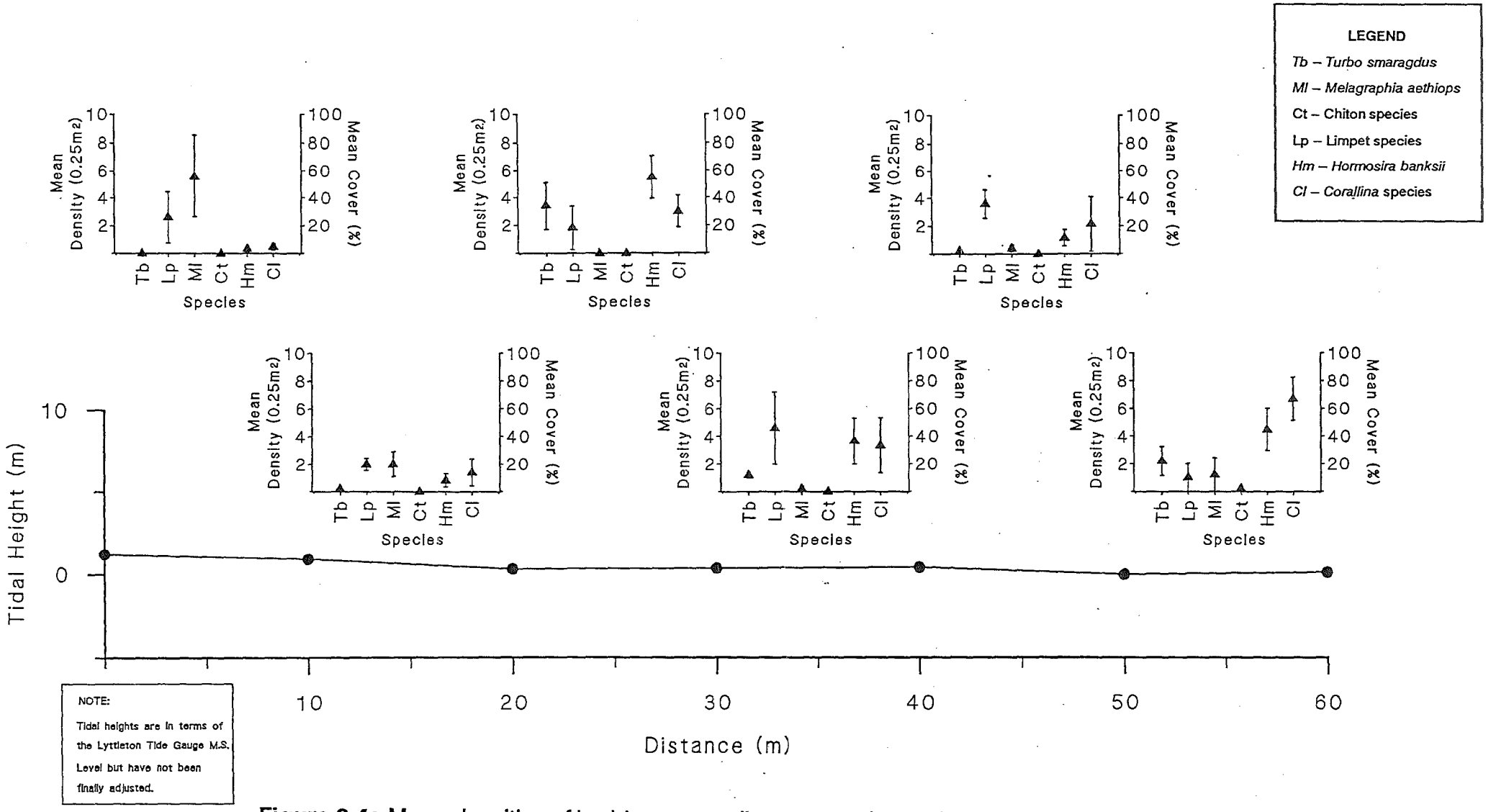


Figure 2.4a Mean densities of herbivorous molluscan species and percentage cover of algal species for each 5x10m section of **Transect B, Spaniards Bay** in January 1991. Error bars are ±1 s.e.

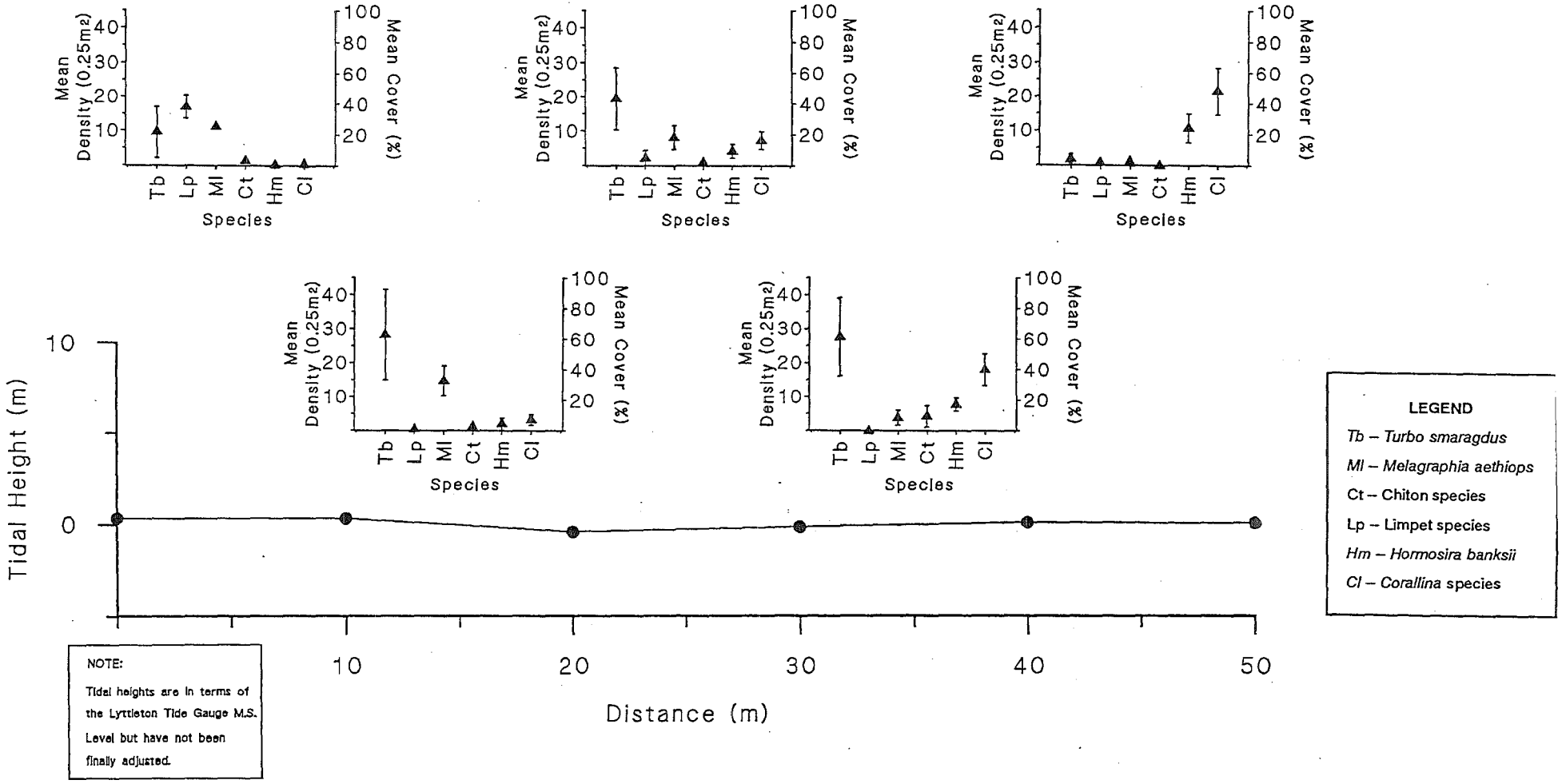


Figure 2.2a Shell length/frequency histograms for each 5x10m section of **Transect C** in the **intertidal, Whakatu Point.**

A correlation matrix of the major species and substratum categories indicates there are no strong associations of *Turbo* with a particular species of algae, herbivore or substratum category **(Table 2.3)**. *Turbo* are slightly negatively correlated to consolidated substratum types, and slightly positively correlated to *Cystophora* species, and less so to pools.

CORRELATION MATRIX FOR ASSOCIATION DATA

	ShHt	Hab2	Hab3	Hab4	Turb	Mel	Limp	Chit	Horm	Corl	Cyst	FRed	Ralf	SmBr
Hab2	0.002													
Hab3	-0.192	-0.762												
Hab4	0.182	-0.033	0.125											
Turb	0.252	-0.174	-0.033	0.143										
Melg	-0.153	-0.015	0.093	0.120	-0.068									
Limp	0.073	0.038	-0.029	-0.009	-0.060	0.237								
Chit	0.062	-0.070	0.113	0.100	0.027	0.337	0.234							
Horm	0.537	-0.022	-0.051	0.131	0.088	-0.120	-0.120	0.005						
Corl	0.620	0.016	-0.124	0.120	0.090	-0.232	-0.163	-0.113	0.641					
Cyst	0.361	0.048	-0.136	0.085	0.315	-0.146	-0.113	-0.055	0.178	0.424				
FRed	0.264	0.142	-0.182	-0.058	0.021	-0.110	-0.085	-0.056	0.146	0.343	0.621			
Ralf	0.269	-0.104	-0.015	-0.099	0.048	-0.063	-0.020	0.118	0.118	-0.037	0.106	0.321		
SmBr	0.251	0.104	-0.135	0.026	-0.043	-0.043	-0.020	0.027	0.097	0.196	0.109	0.072	0.080	
Gren	-0.199	0.022	0.005	-0.090	0.153	0.153	-0.061	-0.048	-0.093	-0.101	-0.055	-0.040	-0.053	-0.049

Table 2.3 Correlation matrix for substratum types, herbivorous molluscs and algal species. Significant values pertaining to *Turbo* are underlined. (ShHt = Shore height, Hab2 = Consolidated substrata, Hab3 = Unconsolidated substrata, Hab4 = Pools, Turb = *Turbo*, Mel = *Melagraphia*, Limp = Limpet sp., Chit = Chiton sp., Horm = *Hormosira, Corl* = Corallina sp., Cyst = *Cystophora* sp., FRed = Filamentous red algal sp., Ralf = *Ralphsia* and SmBr = Small brown algae sp.)

e) Sub-littoral densities and associations.

Sub-littoral populations of *Turbo* occur at Spaniards Bay to depths of 6.15m, extending 40m from the upper margin of the sub-littoral. Densities of *Turbo* observed in the sub-littoral are less than those in the lower eulittoral of the intertidal transects from which they were extended. Maximum mean densities of *Turbo* were 1.4 per 0.25m^2 at a depth of 3m in transect A **(Figure 2.5a)**, 0.6 per 0.25m^2 at depths of 6m in transect C **(Figure 2.5c)**, while no *Turbo* were found in transect B **(Figure 2.5b)**. *Turbo* in these sub-littoral populations were large, with shell lengths ranging between 30-45mm. Although sub-littoral associations were not statistically analyzed, *Turbo* generally occurred amongst coralline turf on the substratum rather than on fronds of large algae. Other herbivorous molluscan species observed at these transects were *Haliotis iris* and *Cookia sulcata.*

At other sites in the Kaikoura region, such as Haumuri Bluffs and Paia Point, sub-littoral *Turbo* with shell lengths ranging between 50-60mm have been observed. They occur in higher densities than at Spaniards Bay, and to depths of at least 9m (*pers. obs.).*

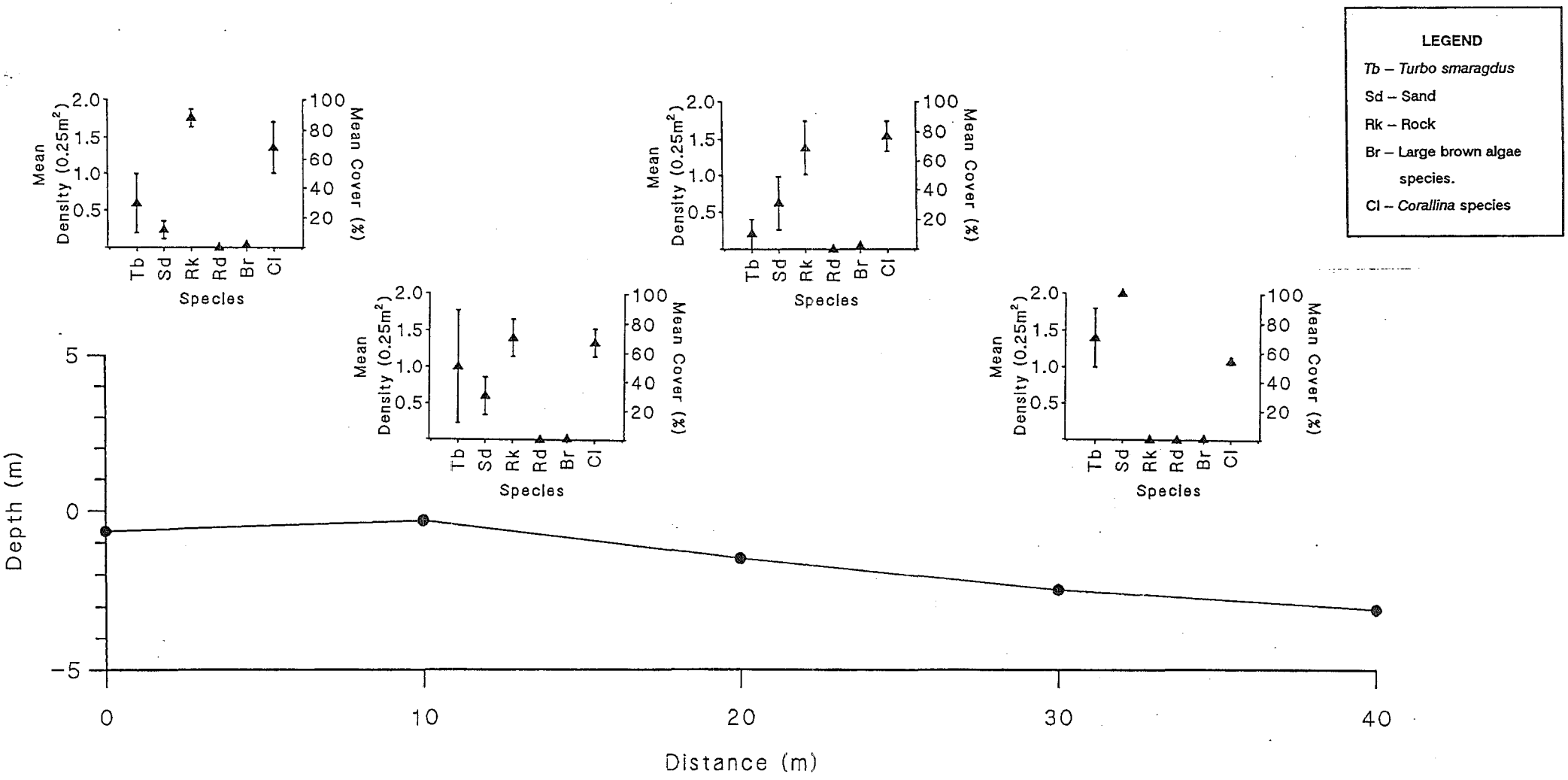


Figure 2.5a Mean densities of *Turbo*, percentage cover of algal species and substratum types for each 5x10m section of **sub-littoral Transect A, Spaniards Bay** in January 1991. Error bars are ±1 s.e.

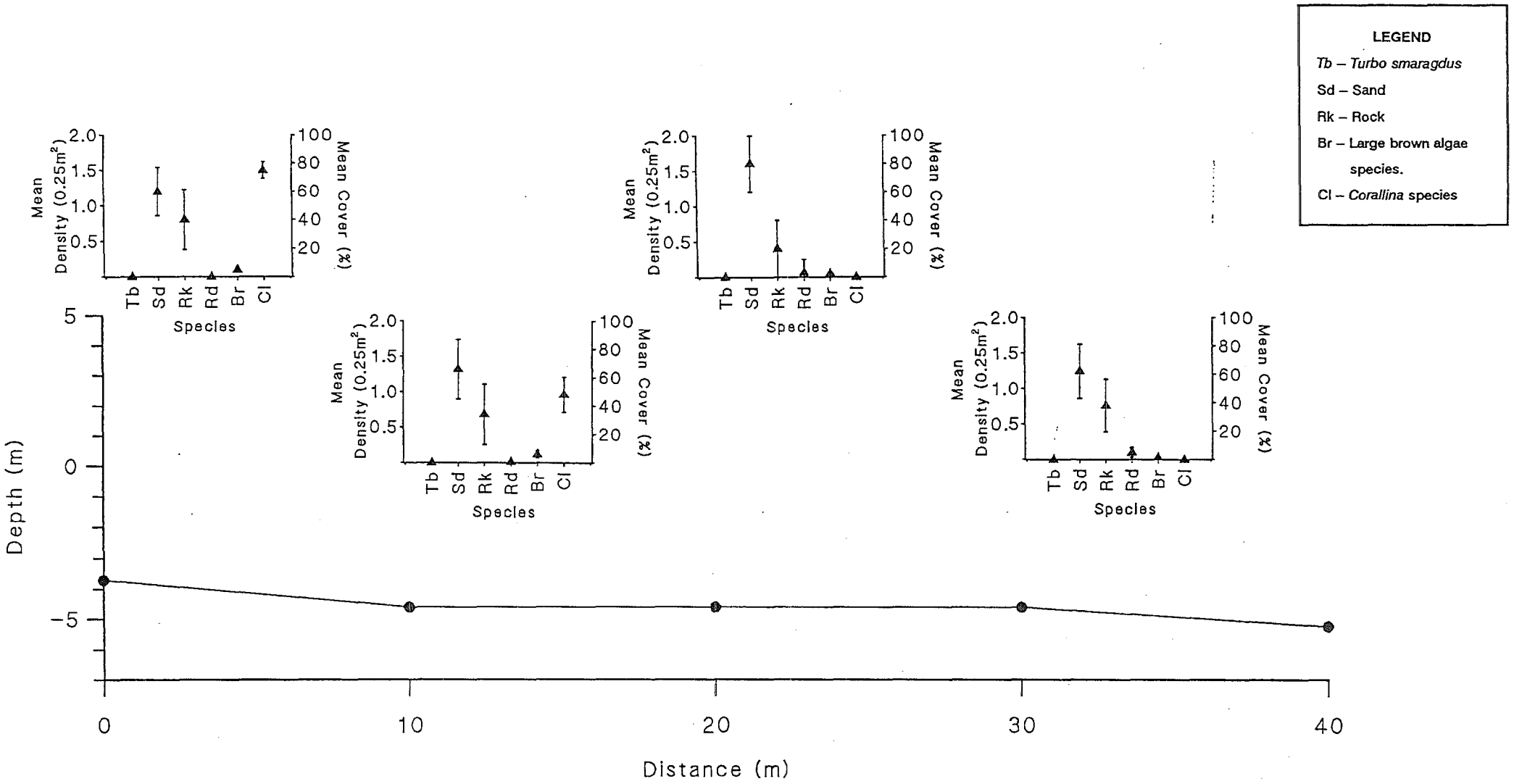


Figure 2.5b Mean densities of *Turbo*, percentage cover of algal species and substratum types for each 5x10m section of **sub-littoral Transect B, Spaniards Bay** in January 1991. Error bars are ±1 s.e.

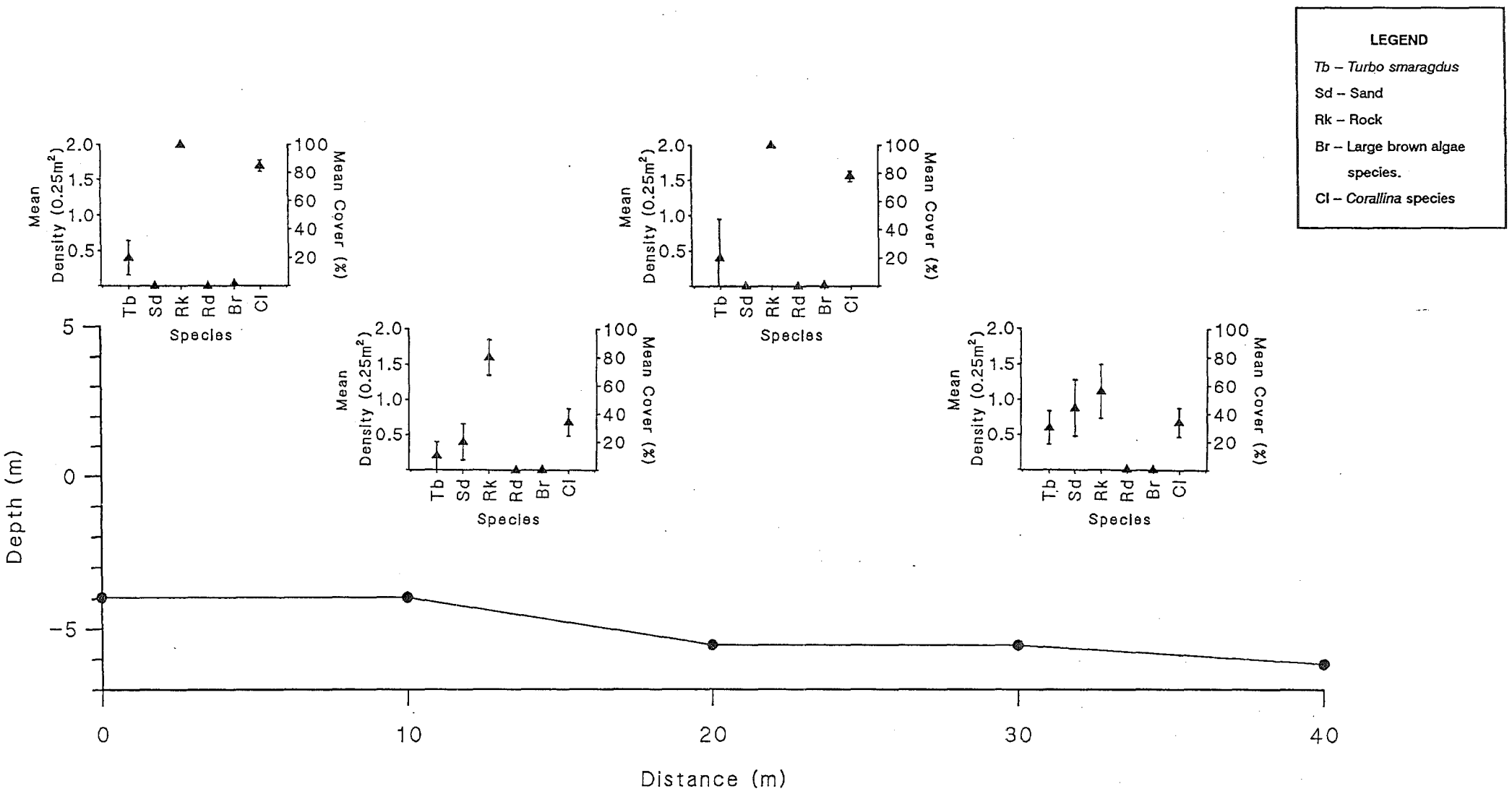


Figure 2.5c Mean densities of *Turbo*, percentage cover of algal species and substratum types for each 5x10m section of **sub-littoral Transect C, Spaniards Bay** in January 1991. Error bars are ±1 s.e.

2.3.2 Temporal Distributions.

a) Length-frequency distributions.

The high shore populations of Avoca Point were predominantly composed of *Turbo* 5-15mm in shell length **(Figure 2.6a)**. Generally, animals 5-10mm occurred at higher frequencies than those 10-15mm in shell length (e.g. August, September and October 1991). Greatest frequencies of *Turbo* 5-10mm were present in August 1991 (n = 125). Other than several in May, few *Turbo* 0-5mm representing new recruits, occurred throughout the sampling period at this shore height. In the mid-shore regions of Avoca Point, the range of predominant shell lengths (5-20mm) was wider than that for high shore regions **(Figure 2.6b)**. The highest frequency of shell length 5-10mm occurred in June (n = 235) and July 1991 (n = 150). *Turbo* of shell lengths 0-5mm occurred in low numbers in April (n = 2), May (n = 18), June (n = 2) 1991 and March 1992 (n = 5) 1992. In the lower regions of Avoca Point, a wide range of shell lengths occurred (0-40mm) **(Figure 2.6c)**. The pre-dominant shell length class varied between months; therefore, it is difficult to make generalisations about the overall pre-dominant size-class.

Turbo did not occur in the high shore sampling area at Spaniards Bay April 1991-March 1992 and therefore, were not plotted. In the mid-shore regions of Spaniards Bay a wide range of *Turbo* shell lengths were present (5-45mm) **(Figure 2.7a)**, generally at lower frequencies than observed at Avoca Point. The largest numbers of most shell length classes occurred in October 1991. Larger *Turbo* (shell lengths 25-40mm) were present in the low shore regions of Spaniards Bay **(Figure 2.7b)**. The predominate shell lengths were generally 35-40mm, which occurred at highest frequency in June 1991 (n = 112). Smaller *Turbo* (<20mm) generally did not occur at this shore height, although several juveniles (5-10mm) were present in April 1991.

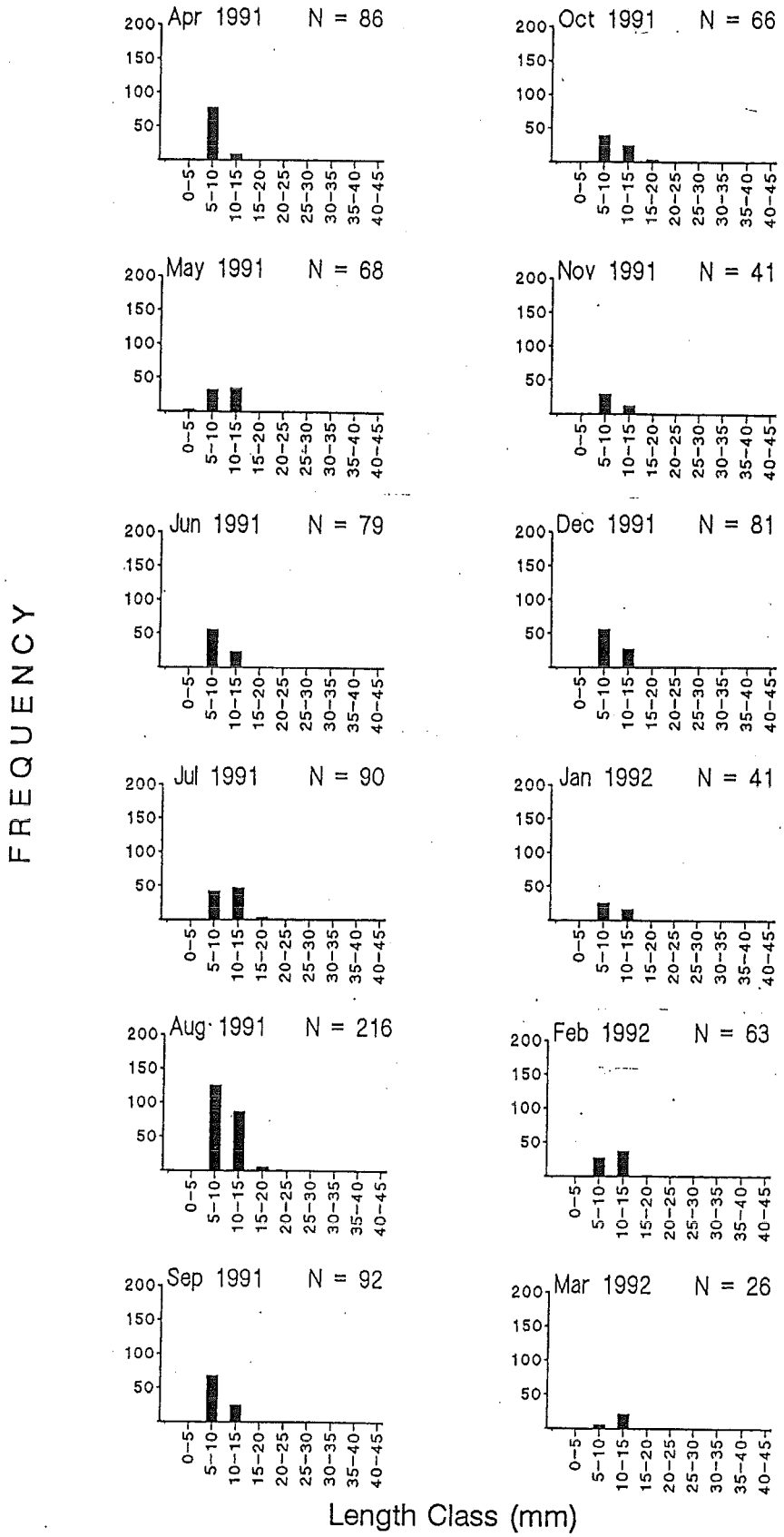


Figure 2.6a Monthly length/frequency histograms for the **high-shore** sampling site at **Avoca Point**. Note that size classes do not overlap (eg. the size class labelled '15-20' represents animals in the size range 15.0-19.9mm).

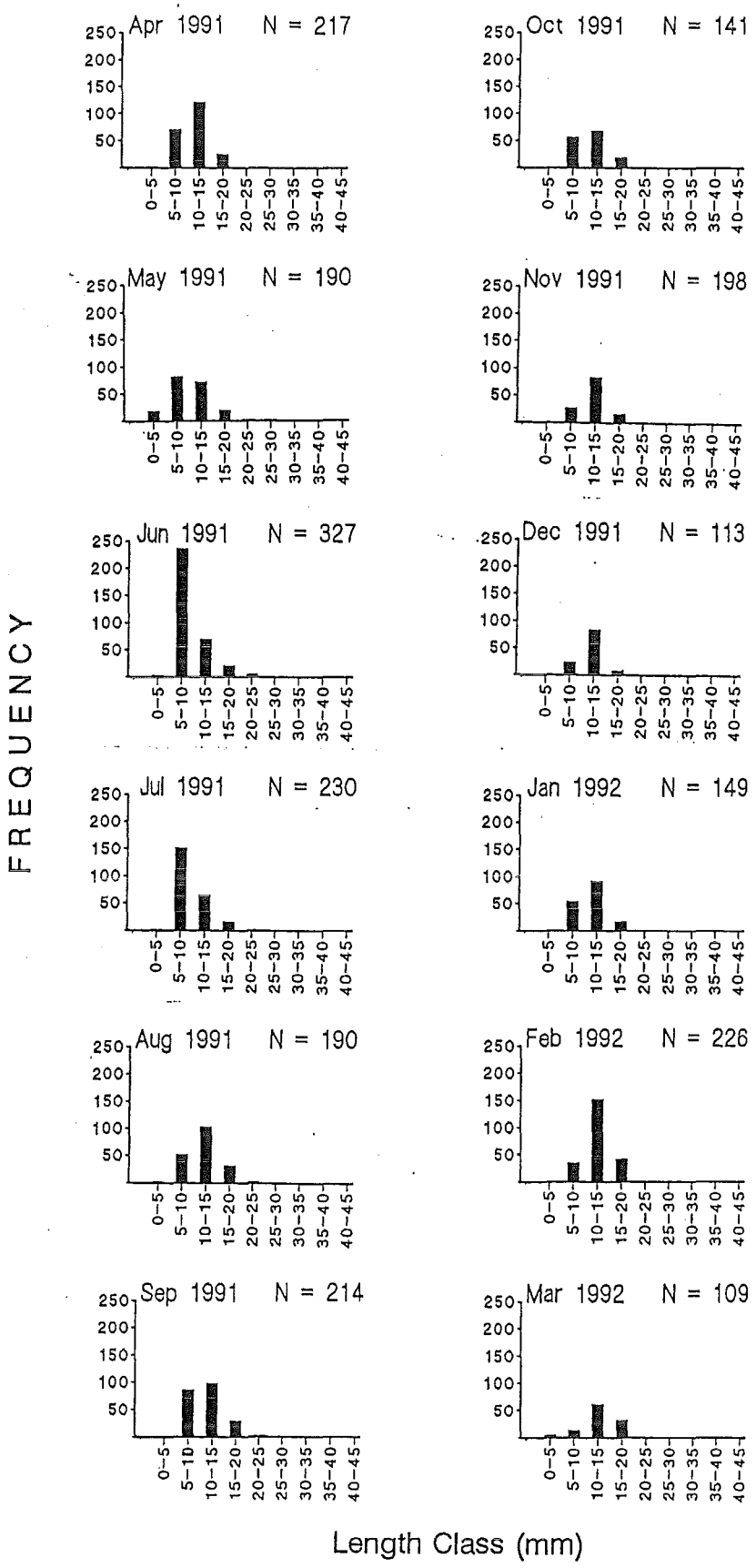


Figure 2.6b Monthly length/frequency histograms for the **mid-shore** sampling site at **Avoca Point**. Note that size classes do not overlap (eg. the size class labelled '15-20' represents animals in the size range 15.0-19.9mm).

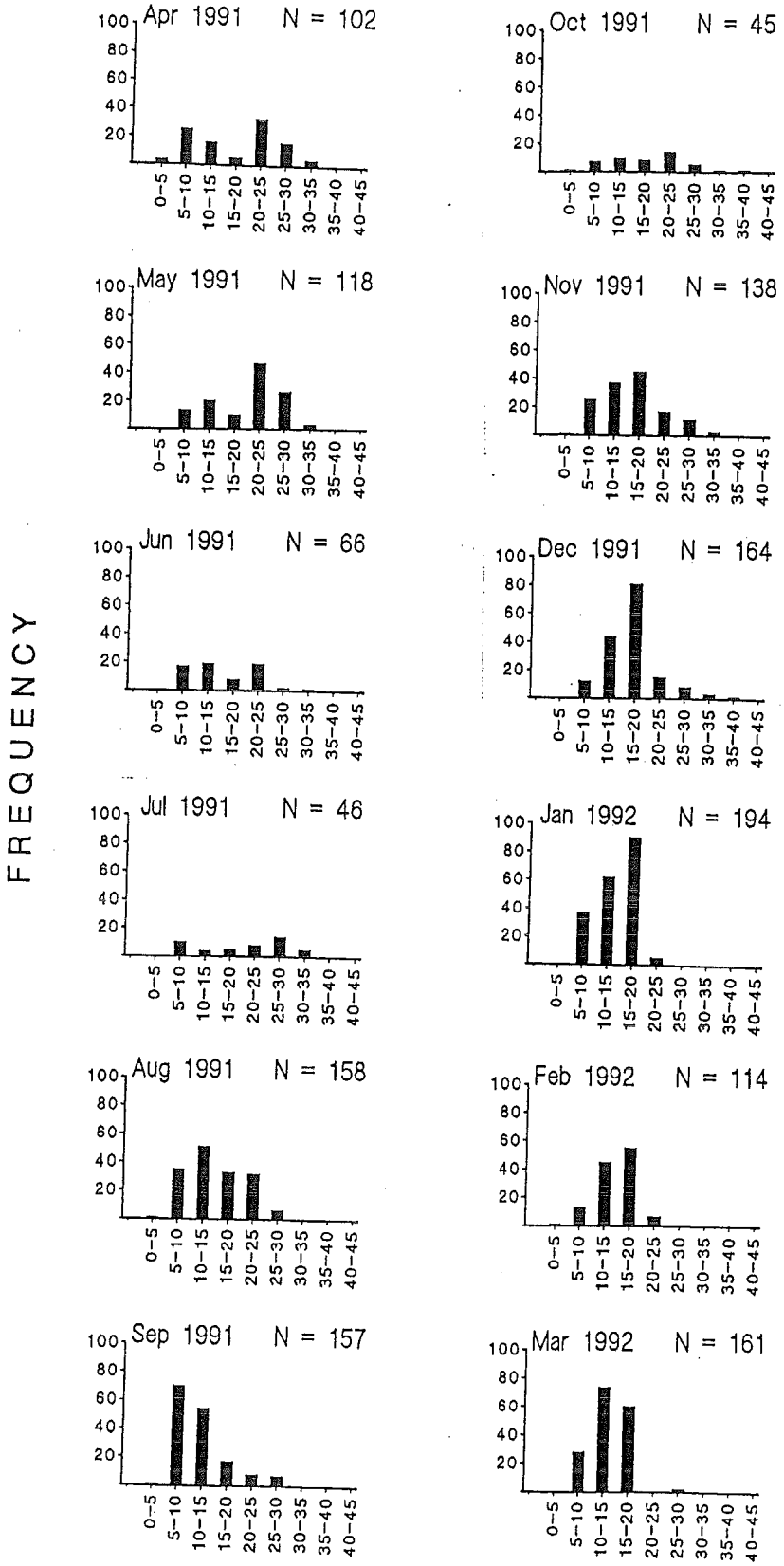


Figure 2.6c Monthly length/frequency histograms for the **low-shore** sampling site at **Avoca Point**. Note that size classes do not overlap (eg. the size class labelled '15-20' represents animals in the size range 15.0-19.9mm).

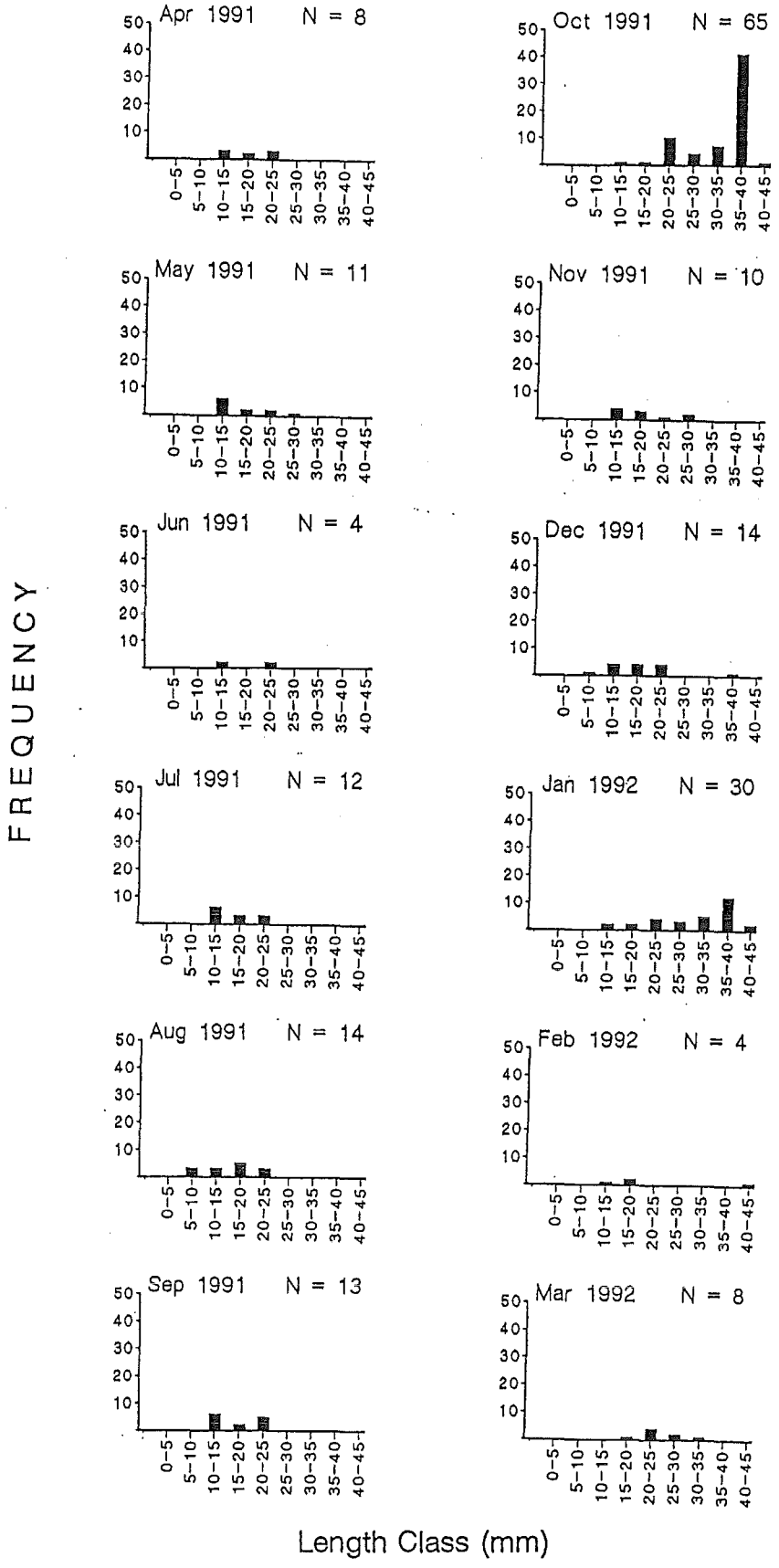


Figure 2.7a Monthly length/frequency histograms for the **mid-shore** sampling site at **Spaniards Bay**. Note that size classes do not overlap (eg. the size class labelled '15-20' represents animals in the size range 15.0-19.9mm).

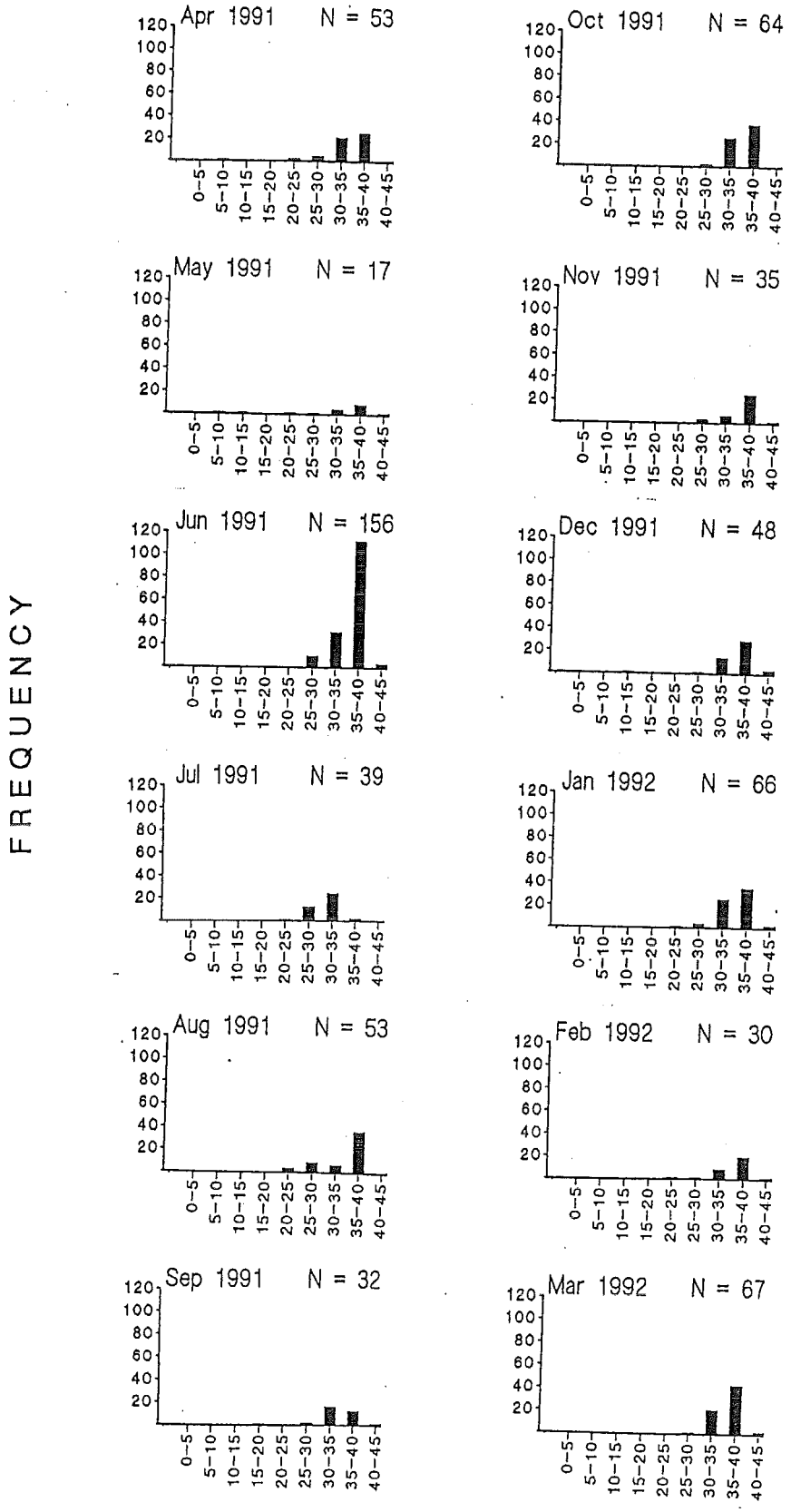


Figure 2.7b Monthly length/frequency histograms for the **low-shore** sampling site at **Spaniards Bay**. Note that size classes do not overlap (eg the size class labelled '15-20' represents animals in the size range 15.0-19.9mm).

b) Overall monthly frequencies.

The mean monthly densities of *Turbo* at shore heights sampled at both Avoca Point **(Figure 2.8)** and Spaniards Bay **(Figure 2.9)** have large error bars (±1 s.e.). This means that finer scaled changes of: **a)** frequency of *Turbo* throughout time at each shore height, and **b)** possible movement of *Turbo* between shore heights, cannot be discerned. However, the results generally indicate that populations at each shore height of both sites were stable throughout the sampling period, with no large intakes of recruits or mass movement of animals down the shore.

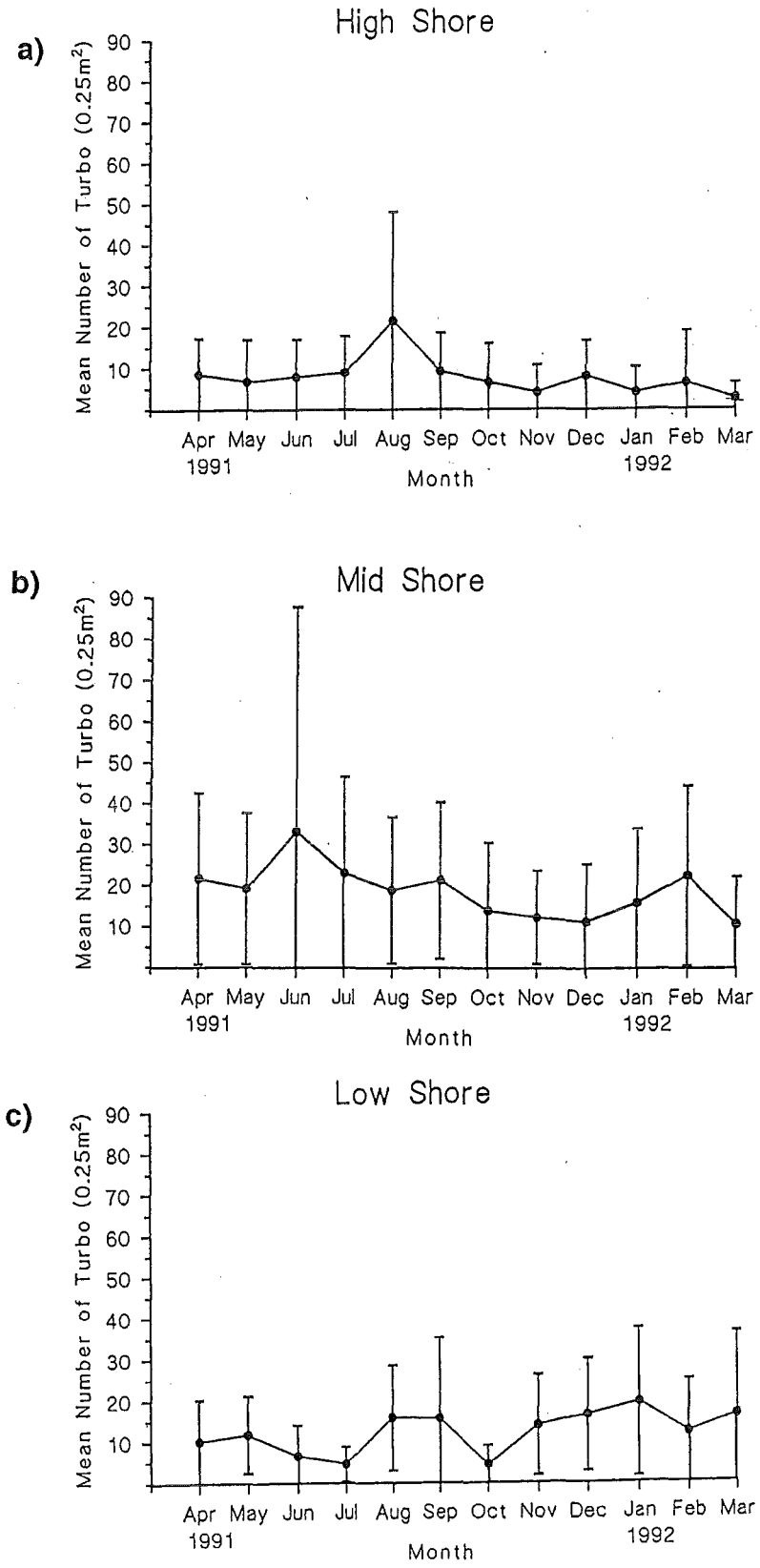


Figure 2.8 Mean monthly numbers of *Turbo* between April 1991 and March 1992 for Avoca Point at: **a)** high, **b)** mid, and **c)** low shore heights. Error bars are ±1 s.e.

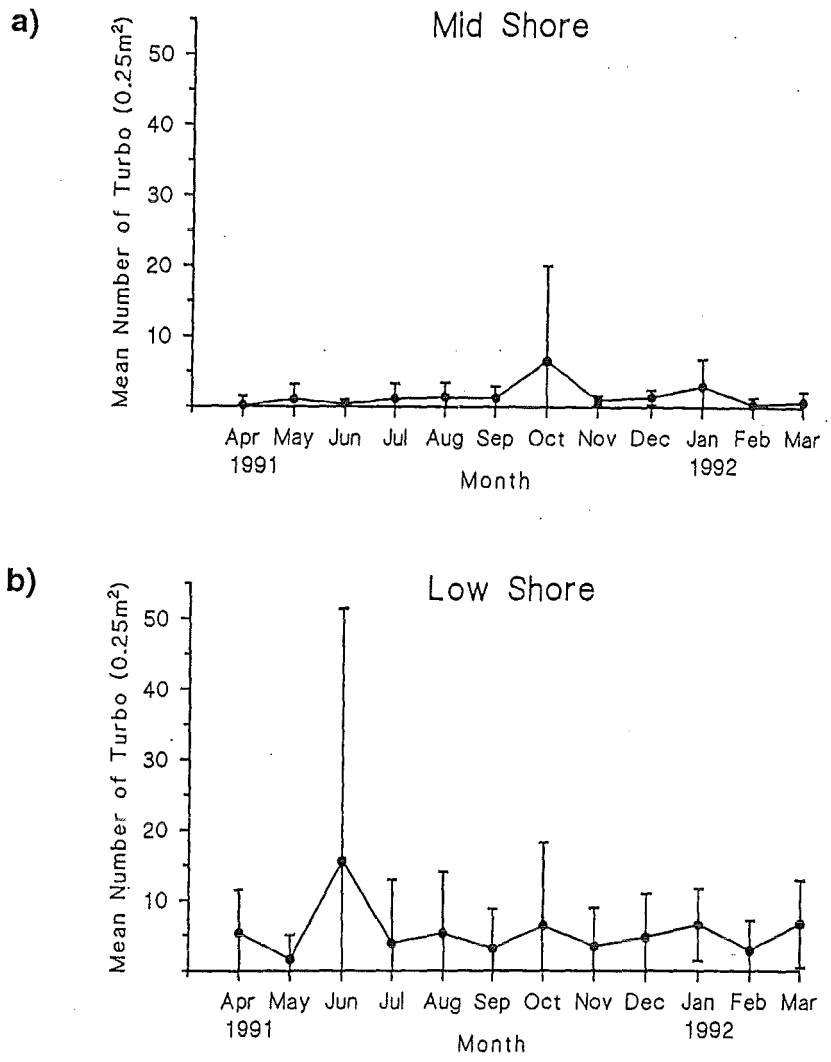


Figure 2.9 Mean monthly numbers of *Turbo* between April 1991 and March 1992 for Spaniards Bay at: **a)** mid, and **b)** low shores heights. Error bars are ±1 s.e.

2.3.3 Recruitment

Of the six patches of coralline turf examined, only one *Turbo* of shell length <5mm was found. This was 4mm in shell length and occurred in a mid shore sample from Avoca Point. An additional two samples, 100x100mm, were taken from this area, but no *Turbo* with shell lengths 0-5mm more were found. A more extensive programme seeking to determine recruitment densities and preferential recruitment substrates and sites was not undertaken when these results were considered in conjunction with the gonad index results (Chapter Five) and temporal sampling results (section 2.3.2).

2.4 DISCUSSION

2.4.1 Spatial distribution - Vertical profile of a shore.

In numbers, Turbo is the dominant and most wide-spread herbivorous mollusc along the vertical profiles of the shores sampled. The broad distribution of *Turbo* reflects the species ability to survive in very different conditions. The upper eulittoral can be subjected to extended periods of aerial exposure and extremes of temperature and desiccation during low tide, while in the sub-littoral, submergence is continuous.

Turbo were observed to have an aggregated pattern of distribution over the shore. The greater proportion of the 0.25m^2 quadrats used to sampled the shore were devoid of *Turbo*, while several quadrats had higher frequencies of *Turbo*, one as many as 77. Aggregated distributions of intertidal molluscs has been observed in many intertidal species (e.g *Nerita atramentosa* and *Bembicium nanum* [Underwood 1976]). Aggregations may result from the migration of many individuals to habitats that are conducive to survival during periods of emergence at low tide. This may include rock pools, damp crevices, and algal fronds; or feeding.

A gradient of *Turbo* sizes and densities occurred along all of the shore sampled. *Turbo* of smaller shell lengths occurred all over the shore, although at higher densities in the mid-eulittoral. The largest individuals were restricted to the sublittoral fringe. Similar gradients were observed at Fergusson Wharf, Auckland (Grange 1974) and Echinoderm Reef, Leigh (Smith 1969, Walsby 1977, Edwards 1982).

The gradient of sizes and migration of *Turbo* down a shore has been described as a function of the effects of waves striking the animal and the shell area exposed to the wave (Walsby 1977). When new recruits reach a critical size, becoming too large to shelter amongst coralline turf, they are dislodged by waves and moved to sites with less wave disturbance and more shelter lower on the shore (Walsby 1977).

The differentiation of shell length distribution down a shore profile may relate to larger individuals having different nutritional requirements than smaller individuals. Of the shores sampled, the mid and high regions had smaller percentages of macro-algae covering the substratum than at lower shore levels. Smaller *Turbo* may be able to maintain their nutritional needs at higher shore levels by feeding on micro-algae and diatoms, whereas larger *Turbo*, probably with higher energy requirements, need to feed in areas of greater food availability.

The size/frequency distribution observed on the Kaikoura Peninsula cannot be explained by physical factors such as desiccation limiting the upper distribution of larger individuals. Smaller animals, having a greater surface-volume ratio than larger animals, are more susceptible to desiccation via evaporation of water from the body tissue than larger animals. If desiccation was the factor limiting the upper distribution of *Turbo*, larger individuals might occur higher on the shore. However, Rasmussen (1965) determined that *Turbo* had a higher tolerance to desiccation than *Melagraphia aethiops*, even though *Melagraphia* occurs almost exclusively from mid to high shore. This suggests that the upper limit of the distribution of *Turbo* on the shore is not determined by desiccation.

2.4.2 Spatial Sampling - Between sites.

Turbo occurred on both rock (eg. Transect B at Spaniards Bay) and sandy substrata (eg. Transect B at Whakatu Point). *Turbo* are more likely to occur on consolidated substrata because sand is likely to reduce the ability of *Turbo* to adhere to the substratum, particularly at sites more exposed to wave action. Where *Turbo* did occur on a sand substratum, the animals were contained by ridges of limestone.

Differences occurred in the distribution of *Turbo* between sites sampled on the Kaikoura Peninsula. For example, densities of *Turbo* were greater at Whakatu Point, particularly transect C, than at either Spaniards Bay or Lighthouse Reef, and were generally comprised of individuals of smaller sizes. Spatial variability in the distribution of a species between sites may be influenced by several factors including: modes of

reproduction and life history strategies, external conditions such as currents, physiological and morphological constraints, physical conditions at each site, inter and intra-specific competitive interactions, locomotory ability, nutritional requirements and feeding modes (Underwood 1979).

Modes of reproduction, especially those species with planktonic larval development, can influence annual and geographic fluctuations in abundance of a population (Underwood 1979). *Turbo* are broadcast spawners, for which fertilisation of gametes and subsequent development of larvae occurs in the water column (Grange 1974). Successful settlement of larvae is dependent on successful spawning and fertilisation of gametes, mortality rates of larvae while in the plankton, dispersal of larvae by water currents, and suitability of conditions at a settlement site. The spatial and temporal variability of these factors can cause variability in quantities of larvae available to settle and recruit into a population, thereby, possibly influencing spatial and temporal variability of a species' abundance.

Turbo are able to exist in exposed areas, such as Paia Point and Haumuri Bluffs, as well as sheltered areas, such as Lab Rocks. *Turbo* have also been reported to occur in mangrove areas in the North Island, that are extremely sheltered and have a mud substratum (Walsby *et al* 1982). Exposure to wave action has been observed to influence the distribution of intertidal organisms (Meyer and O'Gower 1963, Lubchenco and Menge 1978), and may similarly influence the spatial distribution of *Turbo* (e.g. Smith 1969). Wave action in the intertidal zones of exposed areas may dislodge *Turbo* which would not be able to reattach, and thus be swept into the intertidal. This hypothesis is supported by the observations of Rasmussen (1965), who observed that *Turbo* are restricted to the sub-littoral zones in exposed areas.

The occurrence of dense stands of algae can also influence the distribution of *Turbo.* Edwards (1982) observed that negligible numbers of *Turbo* occurred in the fucoid fringe, despite greatest numbers of *Turbo* occurring immediately above the fringe on Echinoderm Reef at Leigh (Edwards 1982). Edwards (1982) proposed that the ability of *Turbo* to adhere to the substratum was limited by dense stands of algae (and so

were swept away by wave action). Although fucoid algal species such as *Carpophyllum* sp. and *Cystophora* sp. do occur on the Kaikoura Peninsula, they are generally not present in a dense band at the upper margin of the lower eulitoral as at Leigh. However, dense patches of large algal species do sometimes occur along sub-littoral margins and in the sub-littoral of the Peninsula, and possibly influencing the distribution of *Turbo* between areas.

2.4.3 Sub-littoral populations.

Low density populations of *Turbo* occur in the sub-littoral at Spaniards Bay on the Kaikoura Peninsula. Shell lengths of these animals are greater than 35mm, which, when corroborated with growth analysis (Chapter 3), suggest that members of sub-littoral populations at Spaniards Bay are at least 5 years in age. Rasmussen (1965) noted that in exposed areas *Turbo* are restricted to the sub-littoral and members of these populations represented age groups beyond three years. Populations of sub-tidal *Turbo* also occur 1-2m below MLWS at Fergusson Wharf, Auckland (Grange 1974), though not below the fucoid fringe at Leigh (Edwards 1982) or in sub-littoral transects below *Carpophyllum* at Whangarei Heads (Smith 1969). Sub-littoral *Turbo* populations in Pelorus Sound have been recorded as occurring at mean densities of 10.24 per m^2 $\pm$ 1.31 standard errors. A maximum density of 31.20 per m^2 occurred in boulder/rubble areas and to depths of 14.6m, with highest densities occurring between 8-10m (Lindsay Chadderton *pers. comm.*).

Sub-littoral populations are likely to occur as the result of wave action dispersing animals from intertidal into sub-littoral areas. Movement back into the intertidal would be restricted at Spaniards Bay by the 1-4m ledge that occurs at the upper margin of the sub-littoral.

2.4.4 Associations.

Turbo are not strongly associated with particular herbivorous molluscs, algal species or substratum types on the shores sampled. However, there is a weak positive correlation between the presence of *Turbo* and *Cystophora* species on the lower shore, and a negative correlation between *Turbo* and consolidated substratum. The nature of the relationship of *Turbo* and *Cystophora* was not explored in this study. It may reflect the preference of *Turbo* for *Cystophora* species as a food source, or merely occur as the coincidence of *Turbo* and *Cystophora* sharing a habitat conducive to their survival. The negative correlation between consolidated substratum types and *Turbo* is likely to have occurred because consolidated substratum often constitutes the higher, more exposed regions of the shore that may be: **a)** less conducive to the survival of *Turbo*, or **b)** an area in which *Turbo* are removed by wave action.

The general absence of strong associations between the species sampled on these shores may be reflect the nature of the shores sampled, which were generally low-lying and gently sloping. Consequently, the distinct patterns of zonation and associations that may occur on steeper shores (which would have a steeper gradient of physical factors that may influence the distribution of shore organisms), are likely to be absent on the shores sampled in this study. However, the absence of strong correlations of *Turbo* with particular organisms of the shore indicates that *Turbo* are able to co-exist with a number of species, possibly as the overall superior competitor.

2.4.5 Temporal distribution.

The populations at each shore height sampled at Spaniards Bay and Avoca Point were stable throughout the sampling period, as indicated by: **a)** temporal length/frequencies, and **b)** mean monthly numbers of *Turbo*, as the standard errors are larger than the variations of the means.

There was a clear gradient of *Turbo* sizes down the shore at both sampling sites between April 1991-March 1992. Walsby (1977) described this gradient as a function of the effects of waves striking the animal and the shell area exposed to the wave (as described in section 2.4.2.). Thus, if juvenile *Turbo* of the same year class have similar growth rates, an influx of *Turbo* with smaller shell lengths could be expected to occur at lower shore levels as the critical size for movement by wave action is attained. However, such mass movement of *Turbo* down the shore was not observed to occur at either Spaniards Bay or Avoca Point.

Large influxes of *Turbo* with shell lengths <5mm did not occur at either site between April 1991-March 1992, which is likely to be indicative of recruitment failure. Factors that may have caused recruitment failure include: **a)** failure of brood stock to spawn, **b)** failure of the planktonic larvae to have reached the shore, and **c)** post-settlement mortality of settlers (Connell 1985).

2.4.6 Recruitment.

Growth studies (Chapter Four) indicate that *Turbo* grow approximately 10mm in their first year. The presence of *Turbo* of shell lengths less than 10mm are considered to be recruits from the previous spawning season.

Juvenile *Turbo* less than 5mm in shell length occurred intermittently, and in small numbers at the three shore sampling levels sampled at Avoca Point 1991/1992. The absence of prominent modes for shell lengths 0-5mm may reflect the cryptic nature of juvenile *Turbo*. Walsby (1977) observed that small *Turbo* are found amongst the fronds of coralline turf, feeding on the epiphytic algae. These are difficult to find because of the debris that can accumulate in the coralline turf and similarities in *Turbo* and coralline colouration. However, based on the assumption that searching techniques were effective, the absence of prominent modes may indicate recruitment failure.

2.4.7 General Comments

The distribution of *Turbo* on the shores of the Kaikoura Peninsula is wide and varied, with weak correlations between it and other intertidal floral and faunal species. The variability of the distribution is influenced by numerous factors as has been discussed and described by various authors. The poor associations may be indicative of the gently sloping shores of the intertidal platforms; therefore, physical gradients that influence the distribution of intertidal organisms are also reduced.

CHAPTER THREE

MORPHOMETRIC RELATIONSHIPS

3.1 INTRODUCTION

An analysis of morphometric relationships can be indicative of the changing ratios of different shell and body parts as an individual grows. This information forms a baseline against which parts of the body can be related to the entire animal, which is particularly useful in species for which several parts are used and marketed separately. For example, some abalone species are bought from fishers by total weight when only part of the meat is actually processed (McShane *et al* 1988).

Morphometric relationships have been determined for gastropod species of commercial interest such as *Haliotis iris* (Poore 1972) and *Haliotis rubra* (McShane *et al* 1988). However, no literature on the morphometric relationships of *Turbo smaragdus* was found other than general descriptions of the appearance of the species (Morton and Miller 1968, Walsby and Morton 1982).

The present study sought to determine morphometric relationships as they pertain to the growth of the shell, operculum, body and gonad of *Turbo smaragdus*.

3.2 MATERIALS AND METHODS

In July 1991 a length-stratified sample of 57 *Turbo* was taken to determine morphometric relationships of *Turbo* in the Kaikoura region. Specimens were collected from the intertidal zone at Lab Rocks and from the sub-littoral at Paia Point. *Turbo* collected from Paia Point tend to be larger than those found on the Kaikoura Peninsula and were included to allow a broader range of sizes to be represented in the sample.

At the laboratory, the *Turbo* were examined for shell ribbing or smoothness. Using either callipers or a measuring board **(Figure 2.1)**, the shell and operculum dimensions of maximum length, height and width were measured to the nearest 0.5mm. Total shell, operculum, wet meat (body tissue) and wet gonad were weighed to the nearest 0.0001gm. Sex was determined from the colouration of the gonad. Female gonads are green, while male are cream (Grange 1974). The dissected meat (body tissue) and gonad of each was placed in a weighed watch-glass and dried in a thermowave oven at 70°C for four days, when a constant weight had been achieved. Constant weights were determined by selecting five individuals representing the size range of the sample, and weighing twice daily. Total dry tissue (body tissue and gonad combined) and dry gonad were weighed to the nearest 0.0001gm.

The relationship of gonad to body weight for each sexually mature *Turbo* was calculated using the formula:

$$\text{Gonad Index} = \frac{\text{Dry Gonad Weight} \times 100}{\text{Total Dry Tissue Weight}}$$ (Gonor 1972)

Linear regressions and exponential curves were fitted to the plots of shell, operculum, meat and gonad dimensions. The gonad indices of both sexes were plotted against shell length and an exponential curve fitted.

3.3 RESULTS

Shell width increases linearly with increasing shell length **(Figure 3.1)**, as does shell height with shell length **(Figure 3.2)**. Total weight (combined shell and wet body weight) increases exponentially with increasing shell length **(Figure 3.3)**, as does wet meat weight **(Figure 3.4)** and shell weight **(Figure 3.5)** when plotted against shell length. Operculum weight and operculum length increase exponentially with increasing shell length **(Figure 3.6** and **Figure 3.7)**. Operculum width increases linearly with increasing operculum length **(Figure 3.8)**. In all cases the r^2 value was ≥0.97. Wet gonad weight increases exponentially with increasing shell length for both sexes (females; $r^2 = 0.71$ and males; $r^2 = 0.77$) **(Figure 3.9)**. Similarly, gonad index also increases exponentially with increasing shell length **(Figure 3.10)**, although there is considerable variation in the data set ($r^2 = 0.275$).

Of the 57 *Turbo* sampled, none were observed to exhibit ribbing of the shell. However, this is not consistent with other casual observations on the Kaikoura Peninsula. For example, *Turbo* shells 15-20mm in length have been found with ribbing, while shells 7mm in length had none.

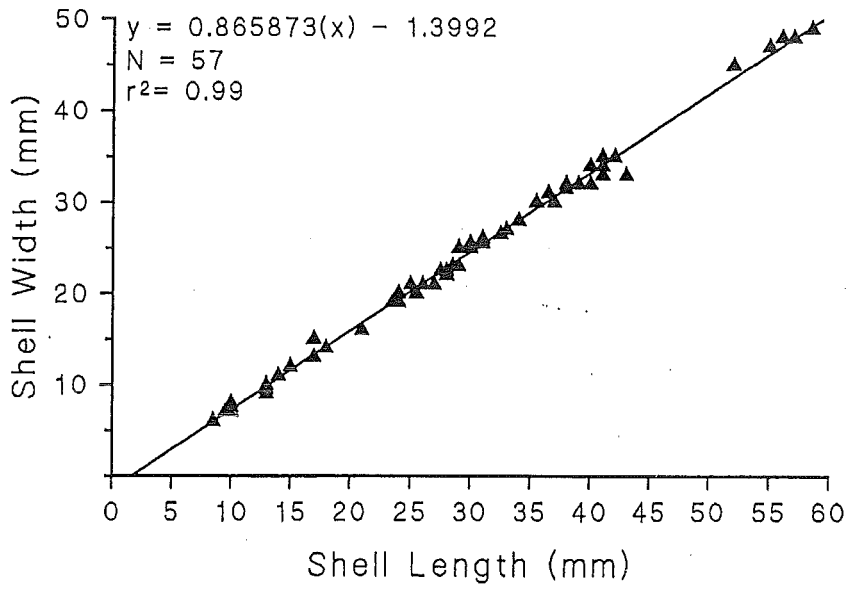


Figure 3.1 Shell width of *Turbo* plotted against shell length, with linear regression fitted.

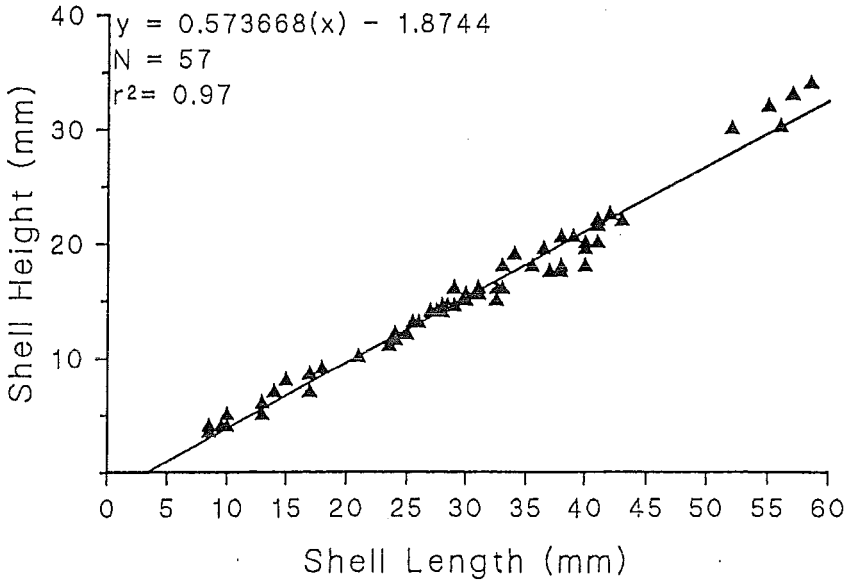


Figure 3.2 Shell height of *Turbo* plotted against shell length, with linear regression fitted.

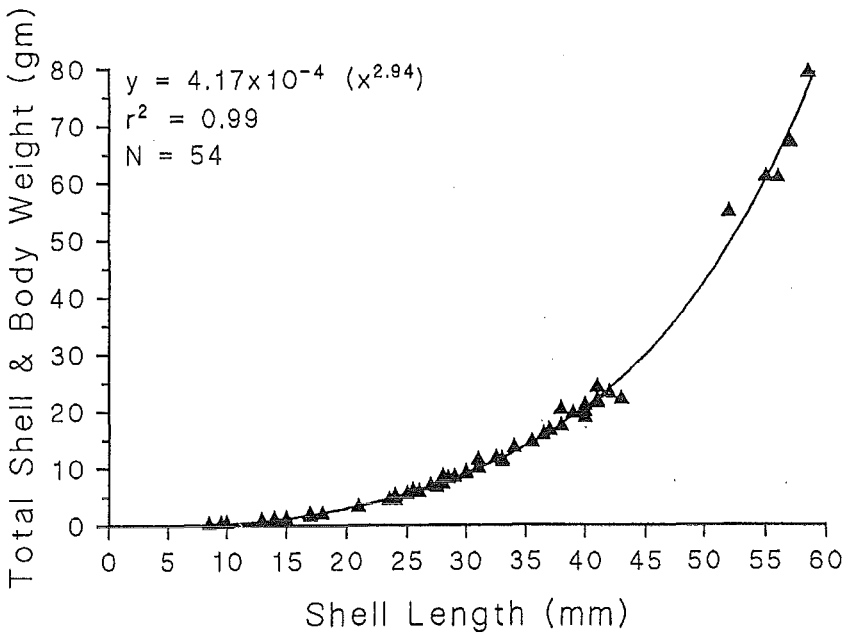


Figure 3.3 Total wet body and shell weight of *Turbo* plotted against shell length.

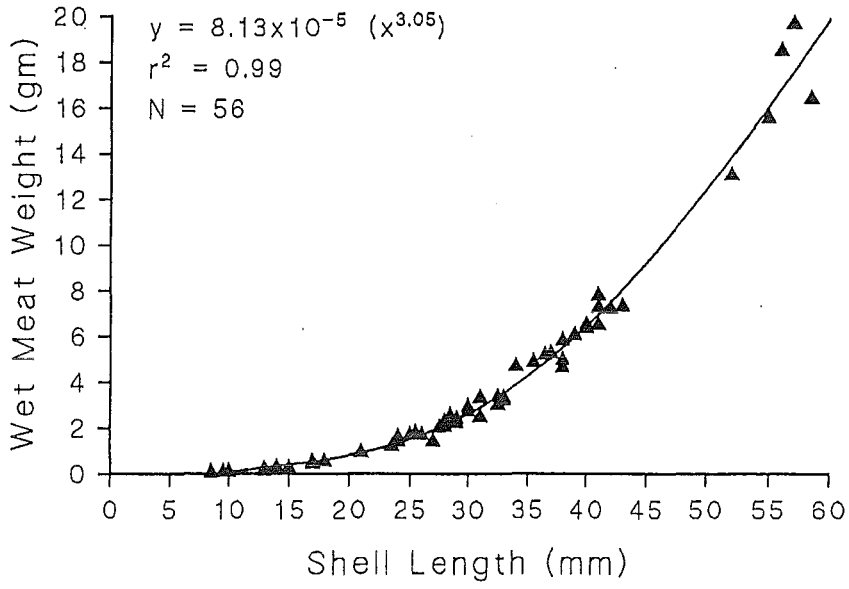


Figure 3.4 Total wet meat weight of *Turbo* plotted against shell length.

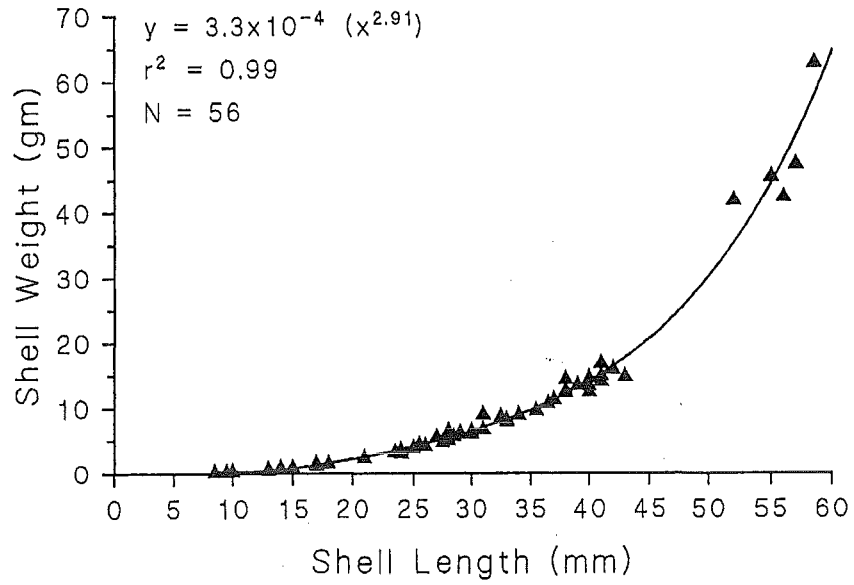


Figure 3.5 Shell weight of *Turbo* plotted against shell length.

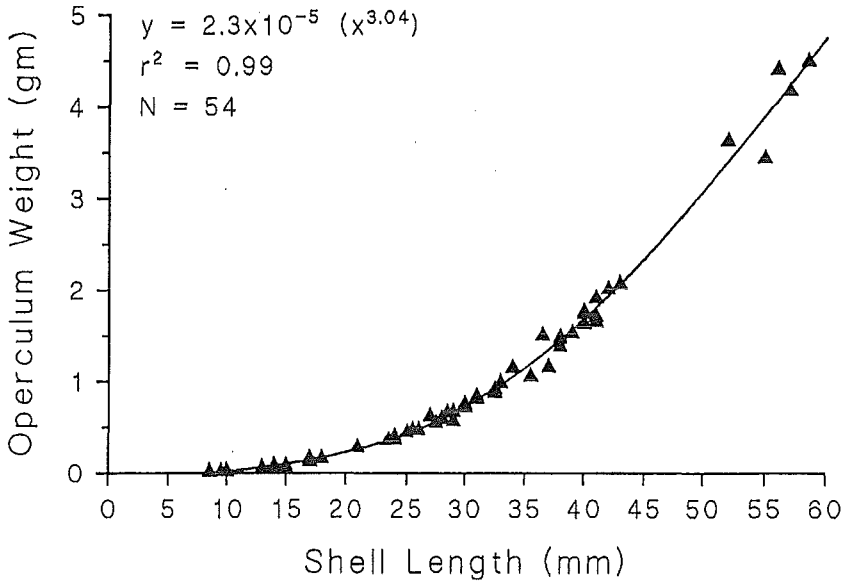


Figure 3.6 Operculum weight of *Turbo* plotted against shell length.

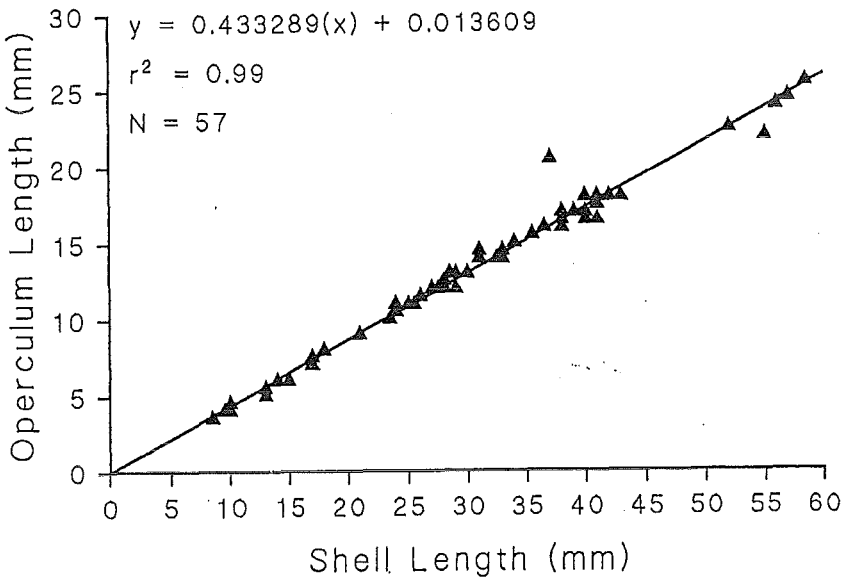


Figure 3.7 Operculum length of *Turbo* plotted against shell length.

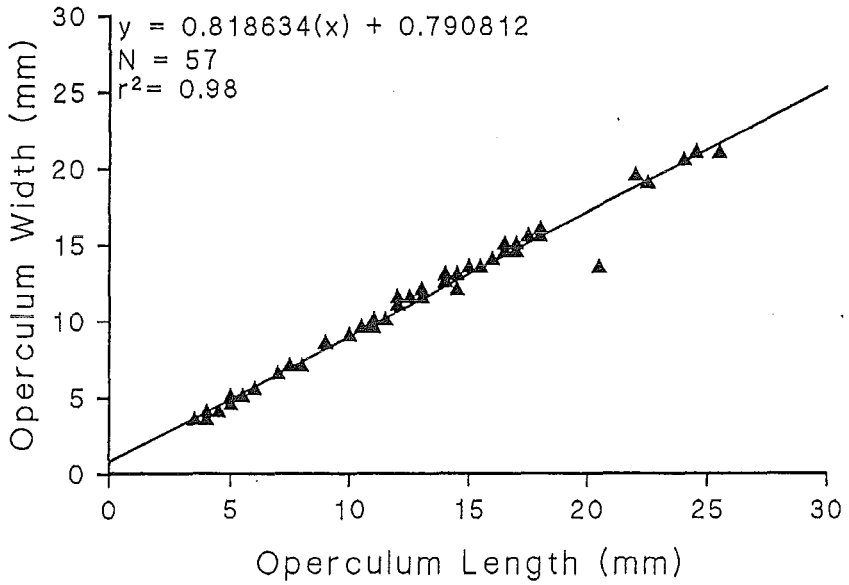
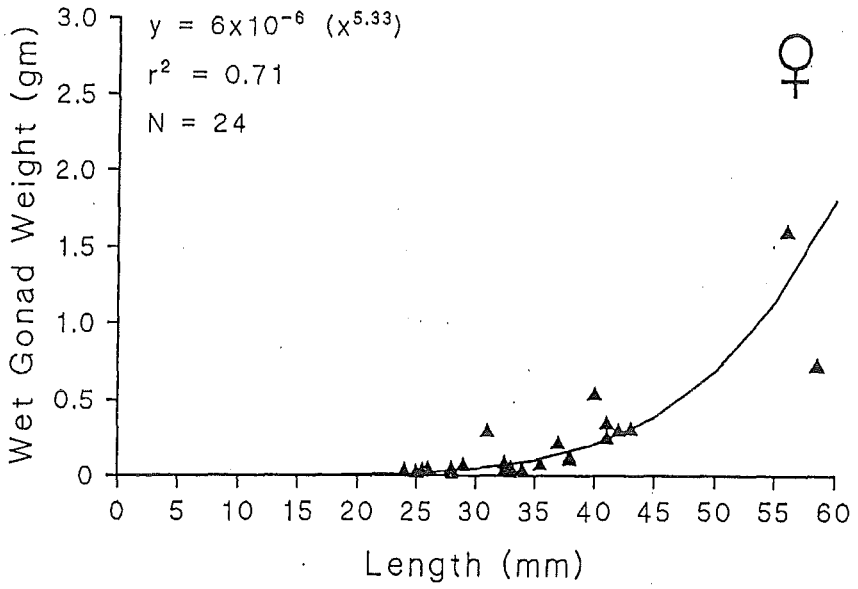


Figure 3.8 Operculum width of *Turbo* plotted against operculum length.

a)



b)

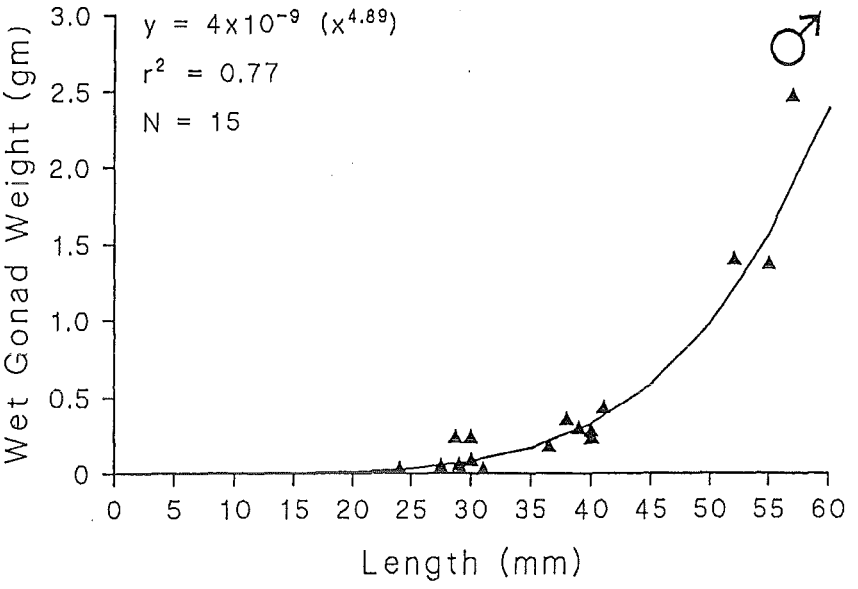
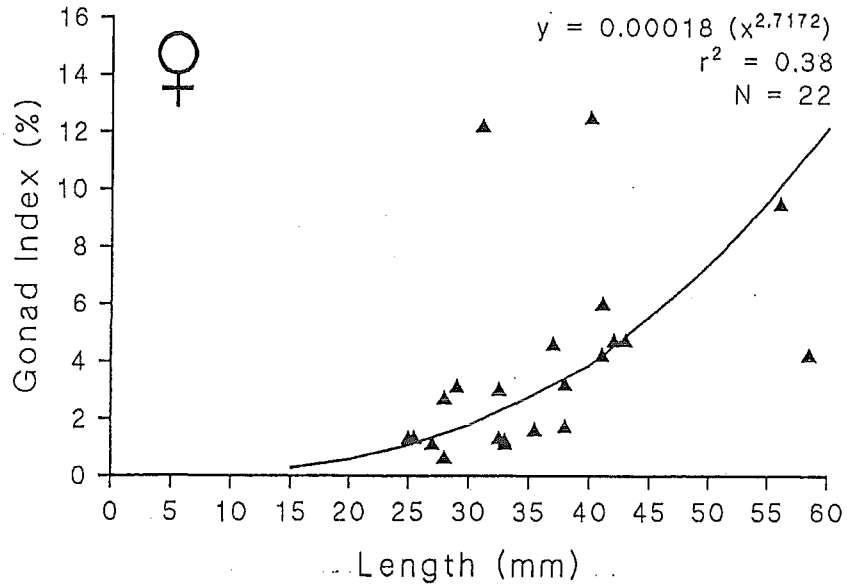


Figure 3.9 Wet gonad weight of *Turbo* plotted against shell length for: **a)** females, and **b)** males.

a)



b)

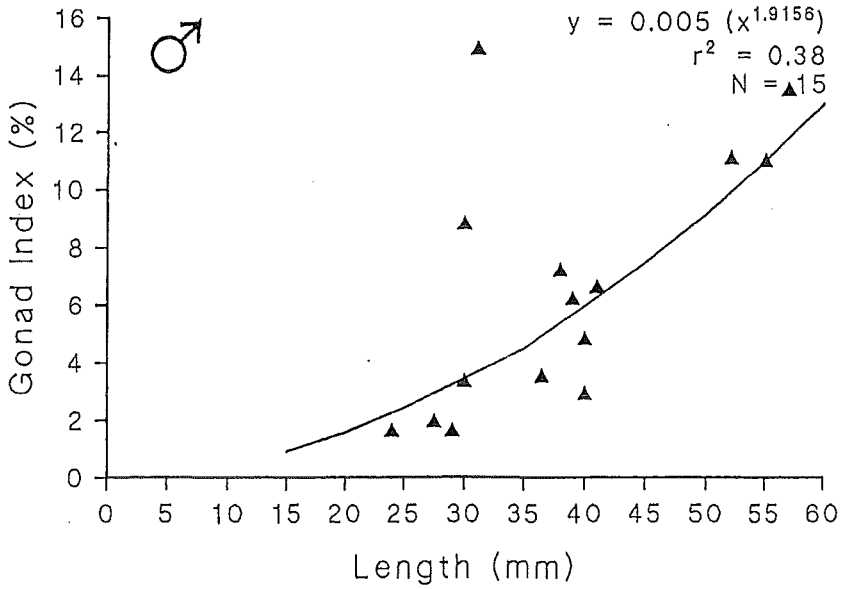


Figure 3.10 Gonad indices of *Turbo* plotted against shell length for: **a)** females, and **b)** males.

3.4 DISCUSSION

Length and height of a shell increase linearly, yet shell weight and meat weight increase exponentially, suggesting that volume was also increasing exponentially. Desiccation is reduced by decreasing surface area to volume ratio, implying that larger, more globular shaped animals are likely to withstand greater desiccation stresses than smaller animals. If desiccation is the limiting factor determining the distribution of *Turbo* on the shore, larger individuals may be expected to occur higher on the shore than smaller individuals. Alternatively, smaller animals, if found in the same vertical zone as larger *Turbo*, may be expected to occupy a different micro-environment than larger individuals. However, results as discussed in Chapter Two, (Patterns of distribution and associations), show otherwise. Although shell lengths of *Turbo* vary vertically on a shore, smaller animals tend to be found at higher shore levels, where desiccation factors would be greater than those of encountered by larger *Turbo* at lower shore levels. Shell shape and size, as it may pertain to desiccation, does not appear to be a determinant of zonation of different sized *Turbo* on the shore. These observations concur with those of Rasmussen (1965), who concluded that desiccation did not limit the upper distribution of *Turbo* because they are more tolerant to desiccation than species such as *Melagraphia aethiops* which occur higher on the shore.

Increasing gonad size with increasing shell length is typical of the increasing investment in reproduction with increasing size/age (Underwood 1972, Grange 1974, Annala *et al* 1987, Wilson 1987). The variability of gonad sizes between the animals sampled suggests that shell length is an inaccurate predictor of gonad size. The variability in gonad indices observed here may be a consequence of sampling in July, when gonads were depleted of gametes. This is discussed more fully in Chapter Five, Reproduction.

Although none of the animals sampled here exhibited ribbing of the shell, shell ribbing of juveniles does occur in *Turbo* populations on the Kaikoura Peninsula. The size at which the *Turbo* change from smooth shell to ribbed shell type is not uniform and not related to the onset of sexual maturation. These results differ from those of Walsby (1977) who observed that shell ribbing occurred in juveniles, changing to a smooth shell form at the size at which sexual maturation occurs.

CHAPTER FOUR

GROWTH

4.1 INTRODUCTION

Estimation of growth rates is a useful tool in determining the age structure and mortality rate of a population. These population parameters are necessary to assess sustainable yields and optimal harvesting strategies for exploited species (Saila *et al.* 1979, McShane *et al.* 1988, Mace *et al.* 1990).

The methods commonly used to assess growth rates include analyses of annual growth checks in shells and otoliths (Francis 1981, Prince *et al.* 1988, Luckens 1990, Massey *et al.* 1990), size frequency modal analyses (Annala *et al.* 1985, Shepherd 1988) and tag-recapture programmes (McKoy et al. 1981, McKoy 1985, Keesing *et al.* 1989). A combination of these methods can be used to verify results (Poore 1972, Sainsbury 1982).

Growth checks can be unreliable indicators of growth and age because of variability in the formation of growth rings relative to the external environment (Prince *et al.* 1988). Assuming tagging has no significant effect on growth, tag-recapture analysis provides information on the variability of the growth of individuals in a population (Francis 1988). Size-frequency analysis is reliant on satisfactory separation of year classes and is therefore generally limited to species with brief annual periods of settlement, rapid growth, and little variation within year classes (Shepherd 1988).

Of these potential methods, only size-frequency analysis has been used to assess growth for *Turbo smaragdus*. Walsby (1977) found that the growth rates of *Turbo* on Echinoderm Reef at Leigh were linear during the first three years and that size classes remained distinct. Grange (1974) found that the size classes of *Turbo* at Fergusson

Wharf, Auckland, also remained distinct, but growth rates declined with increasing size of the animals.

The purpose of the present study was to determine growth rates of adult and juvenile *Turbo* at two sites on the Kaikoura Peninsula using both size-frequency and tag-recapture methods. Mortality was to be estimated from the number of tagged living and dead *Turbo* recaptured during the release program.

4.2 MATERIALS AND METHODS

The growth rates and size structure of *Turbo* populations at Spaniards Bay and Whakatu Point, **(Figure 1.2)** were determined by length frequency analysis and tag recapture.

4.2.1 Length-Frequency.

The length-frequency of *Turbo* populations selected for tag-recapture at Spaniards Bay and Whakatu Point were assessed during 7-12 November 1990 and 22-24 January 1992. A 0.25m^2 quadrat was used to sample each of the two areas randomly. Within each quadrat, *Turbo* were collected and shell lengths were measured to the nearest 1.0mm. Quadrats were repeated until numbers of *Turbo* were sufficient for clearly distinguishable modes in length-frequency plots ($n \geq 450$ at Spaniards Bay and $n \geq 600$ at Whakatu Point).

4.2.2 Tag-Recapture.

Spaniards Bay and Whakatu Point were chosen as tag-recapture sites because of the presence of channels that would presumably restrict the lateral movement of the animals, thereby giving a higher probability of recapture. *Turbo* 7.0-41.5mm in shell length were collected from each site, taken to the laboratory and kept in running seawater. The shell length of each was recorded to the nearest 0.5mm and an

individually numbered tag attached to the shell. To reduce stress due to handling, *Turbo* were kept in tanks of running sea water at ambient temperature for several days prior to release.

One of three types of tag were attached to the shell of each *Turbo*: adhesive paper, lightweight waterproof paper and enamel paint **(Figure 4.1)**. The two paper tag types were laser printed with a number and attached to the shell with superglue, completely covering the tag. For the third tag type, a fine brush was used to apply numbers to the shell with enamel paint, which was then covered with superglue. To estimate tag loss, 271 individuals were double-tagged with a circle of enamel paint adjacent to the primary tag. A further ten *Turbo* labelled with both paint and paper tags were retained in seawater at the laboratory.

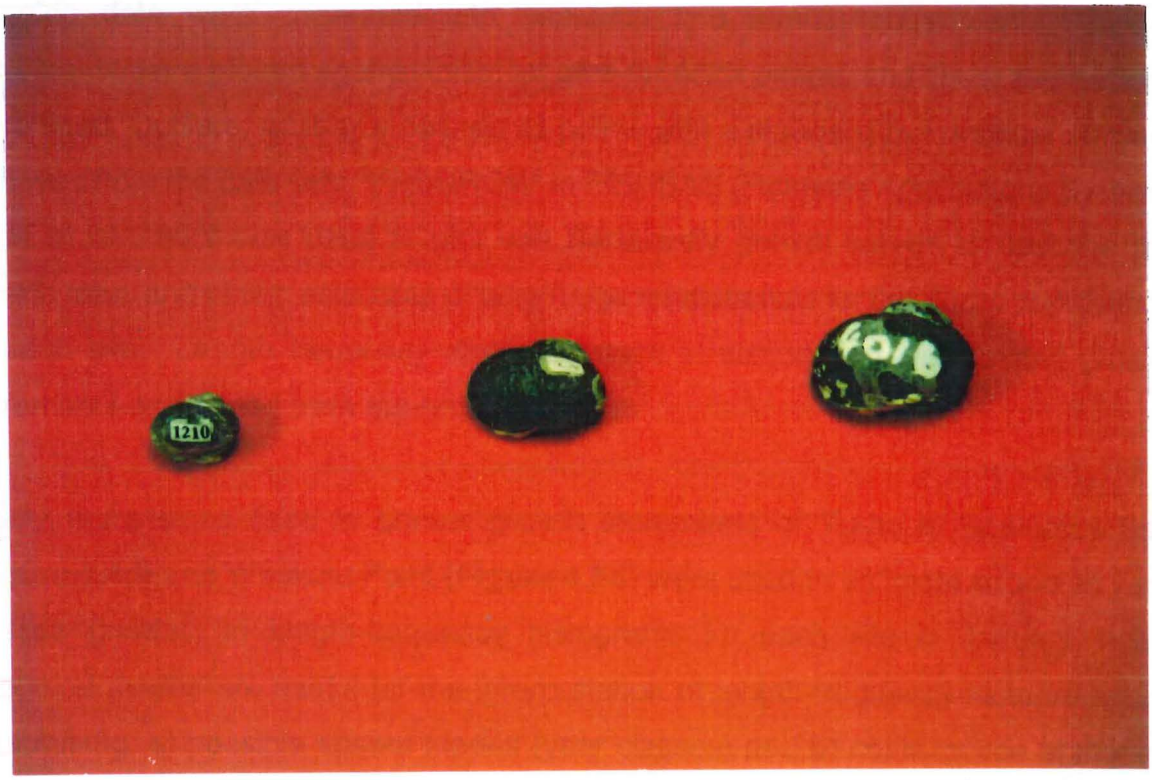


Figure 4.1 The three tag types used to number *Turbo* for tag-recapture after 8-12 months in the field; adhesive paper (left), plastic paper (middle) and enamel paint (right).

Turbo with adhesive paper tags were released to their sites of original capture between 7-12 November 1990. A total of 468 *Turbo* were released at Spaniards Bay and 598 at Whakatu Point. Of these releases, 114 at Spaniards Bay and 157 at Whakatu point were double tagged. On 31 March 1991, a further 127 and 60 animals, tagged with water-proof paper or with numbers painted with enamel paint, were released at Spaniards Bay and Whakatu Point, respectively.

A search to monitor tagging mortalities and tag condition was conducted at Spaniards Bay in December 1990. Comprehensive searches were done at both sites in March, August and November 1991. Using a grid search pattern, release sites and adjacent areas were inspected for living tagged *Turbo* and tagged empty shells. The lengths of these individuals were recorded *in situ* and the animals re-released.

Tagging data were separated into seasonal and annual components. Growth increments were plotted against initial lengths for each period, and linear regressions were fitted. Outliers, arbitrarily defined as points with a standardized residual >3 were removed from the data sets. 'FABGROW' in FISHSAS (Fisheries Applications System, Saila *et al.* 1988) was used to plot von Bertalanffy growth curves to describe the growth rates and obtain estimates of length/age relationships for the *Turbo* populations at each site. Length frequency data was used in conjunction with annual growth increments as derived from tag-recapture data.

Linear regressions fitted to annual growth increments of *Turbo* at Spaniards Bay **(Figure 4.4d)** and Whakatu Point **(Figure 4.5d)** were used to estimate expected year classes (modes) in length-frequency histograms for each site in January 1992. Expected modes are useful for the interpretation of length-frequency histograms for determining: **a)** possible absent modes (year classes) and **b)** coalescence of modes (year classes).

4.3 RESULTS

4.3.1 Length-Frequency

Length frequency histograms of *Turbo* populations at Spaniards Bay **(Figure 4.2)** and Whakatu Point **(Figure 4.3)** show prominent modes in both December 1990 and January 1992. At Spaniards Bay in December 1990, one mode occurred at 13-14mm, a second at 18-22mm and a third at 26-29mm. At Whakatu Point the first distinguishable mode occurred at 10-12mm, the second 15-19mm, the third at 21-24mm and another possible mode at approximately 36mm.

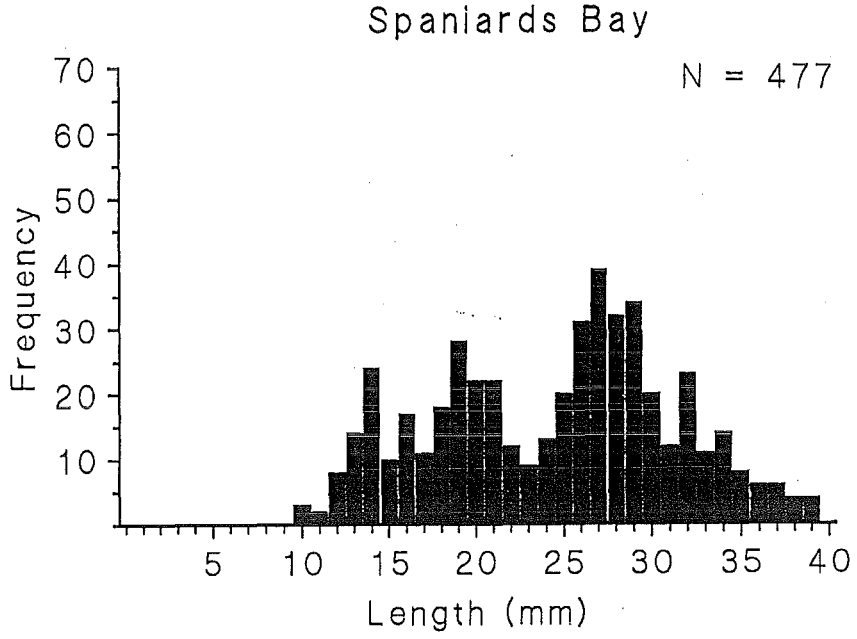
In January 1992 at Spaniards Bay, the first mode occurred at shell lengths of 12-15mm, a second at 22-28mm and a third mode occurred at 33-35mm. The first and second modes at Whakatu Point are more clearly defined than those of Spaniards Bay, the first occurring at 8-14mm, the second at 22-29mm and a third mode between 34-36mm.

4.3.2 Tag Recapture

After three months in laboratory conditions, paper tags lifted from shells, especially when exposed to periods of drying then re-submergence. As a consequence of these observations additional *Turbo* were tagged with waterproof paper and enamel paint and were released in March 1991. Substantial deterioration of the print on waterproof paper tags occurred after several weeks in both field and the laboratory tanks. However, no deterioration was noted of painted tags within five months of release in the field, although after eight months in the field some became difficult to read.

Tagged, living *Turbo* (n=255) were recovered in the December 1990 search at Spaniards Bay. The tags were readable and were well adhered to the shell. Six dead, tagged *Turbo* were found. Two *Turbo* were being consumed by the whelk *Cominella maculosa*, and four shells were occupied by hermit crabs, *Pagurus novaezealandiae.*

a)



b)

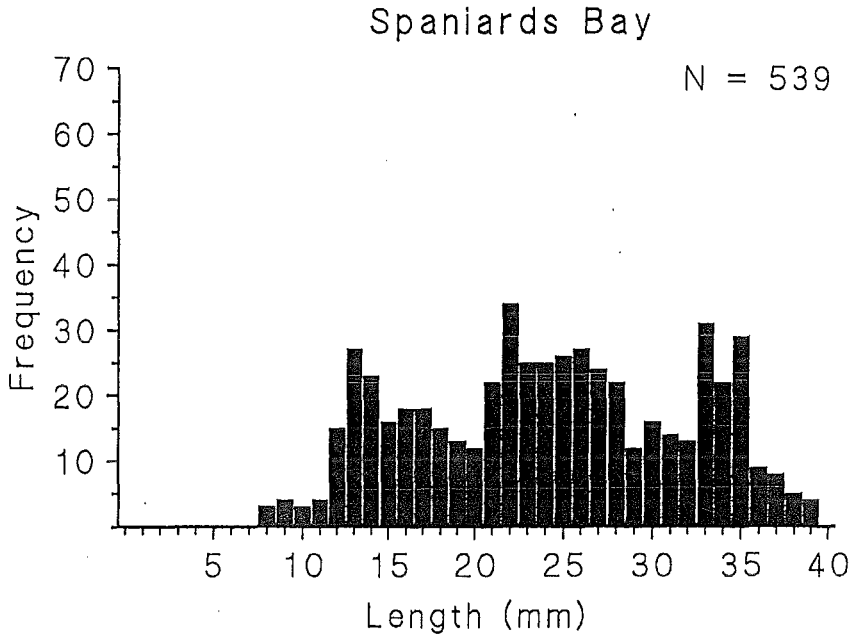


Figure 4.2 Length-frequency histograms for the *Turbo* population at Spaniards Bay in: **a)** December 1990 and **b)** January 1992.

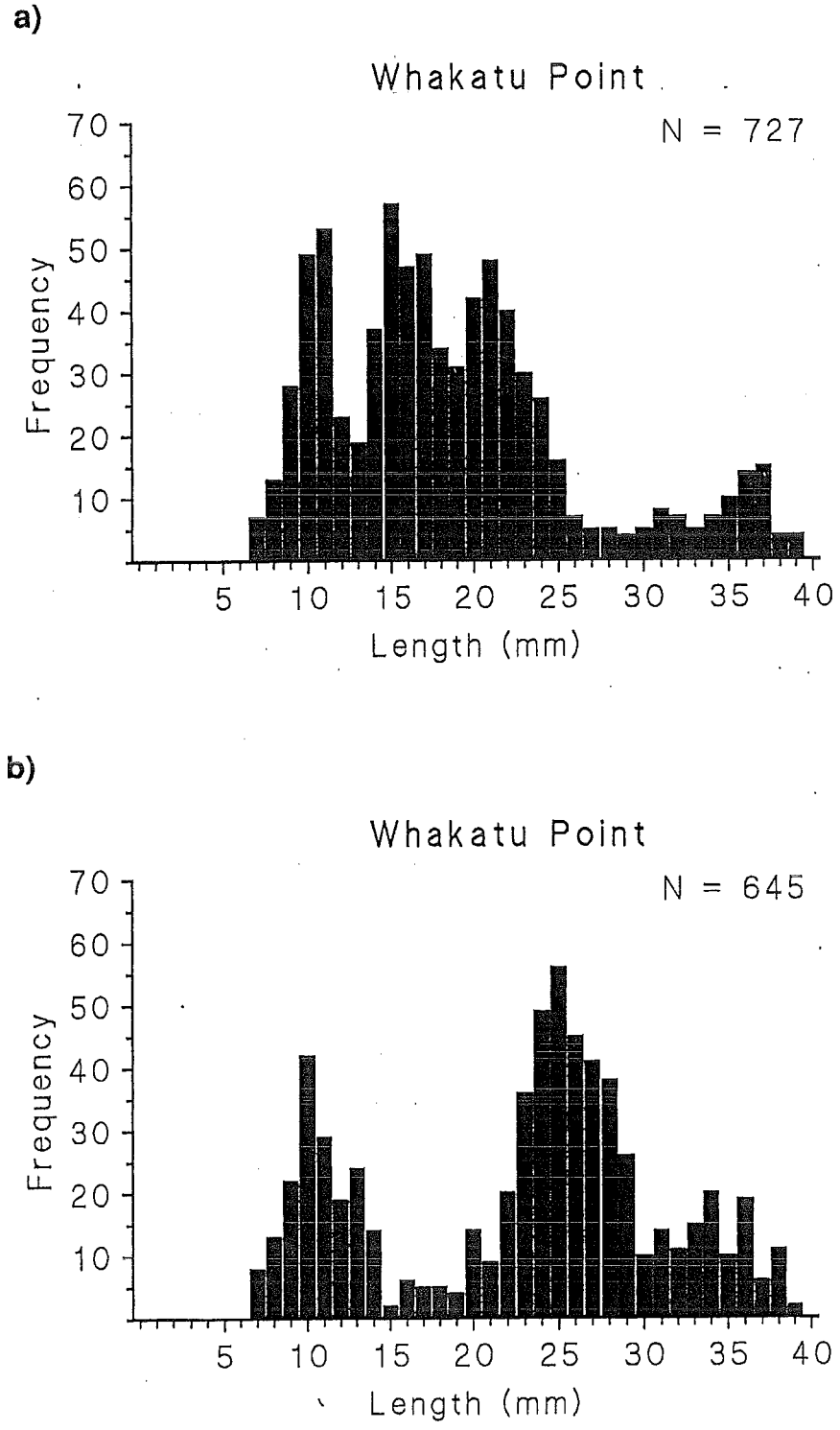


Figure 4.3 Length-frequency histograms for the *Turbo* population at Whakatu Point in: **a)** December 1990 and **b)** January 1992.

Numbers of *Turbo* recaptured varied between each search in 1991 **(Table 4.1)**. Percentage recovery of *Turbo* at one year was 6.5% at Spaniards Bay, and 16% at Whakatu Point. The primary tag was not absent on any of the double tagged individuals.

Table 4.1 Numbers of tagged *Turbo* released and recaptured at Spaniards Bay and Whakatu Point.

SITE	DATE OF FIRST RELEASE	NUMBER RELEASED	NUMBERS RECOVERED 1991		
			March	August	November
Spaniards	Nov '90	468	111	11	30
	Mar '91	127	----	13	22
Whakatu	Nov '90	598	199	18	95
	Mar '91	60	----	3	18

Linear regressions of growth increment against initial shell length for Spaniards Bay and Whakatu Point show that in all but the August to November plot for Whakatu Point, which represented only three *Turbo*, growth rates decreased with increasing size **(Figures 4.4** and **4.5)**. Growth rates at both sites were greater during the period of November-March than during the other periods of the year. For example, at Spaniards Bay, *Turbo* with an initial length of 20.0mm had an average growth of 4.5mm in shell length during November 1990-March 1991, 1.25mm during March-August 1991, and 1.50mm during August-November 1991.

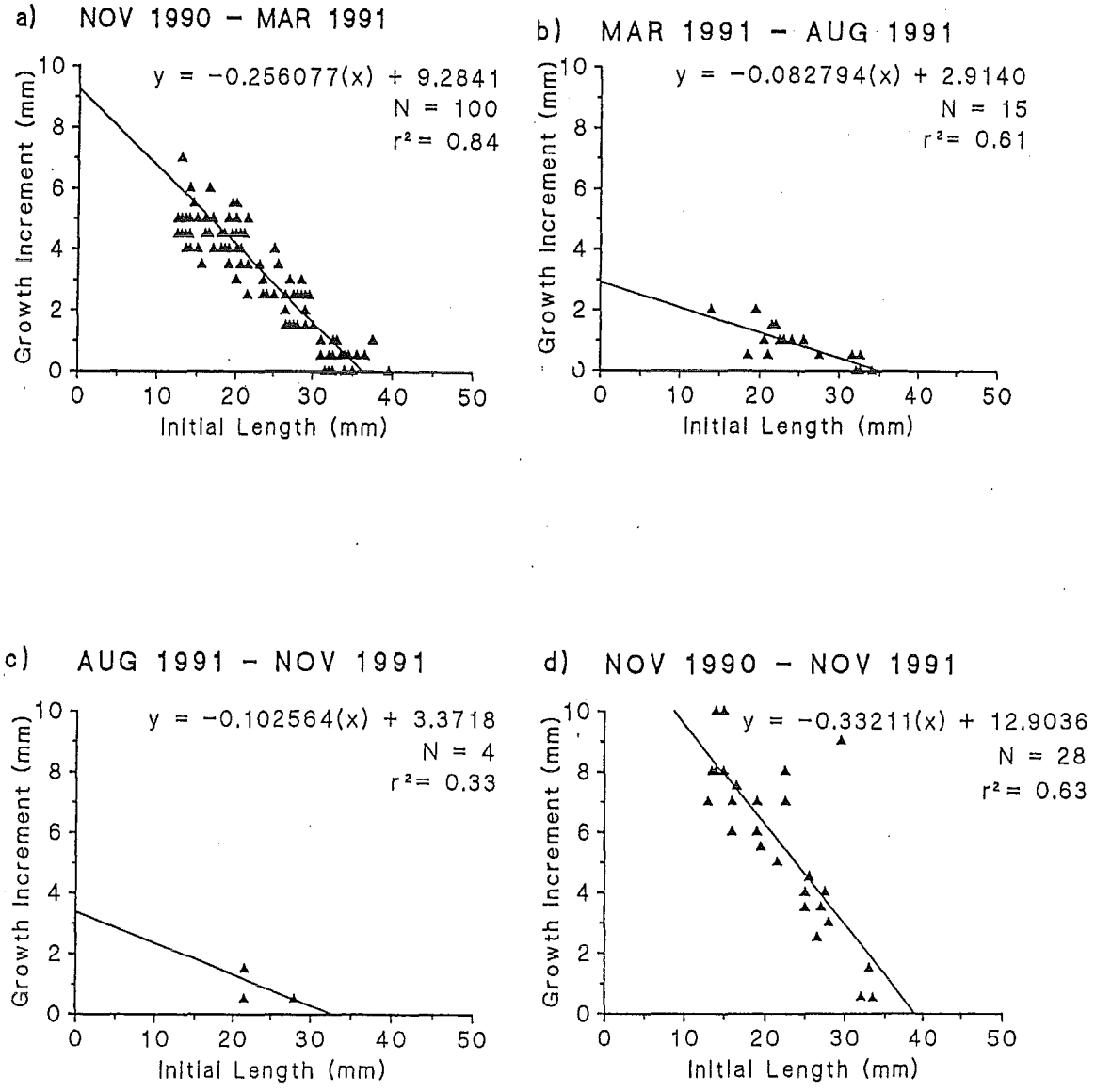


Figure 4.4 Growth increment versus initial shell length from tag-recapture data at Spaniards Bay for: **a)** November 1990-March 1991 **b)** March-August 1991 **c)** August-November 1991 **d)** November 1990-November 1991.

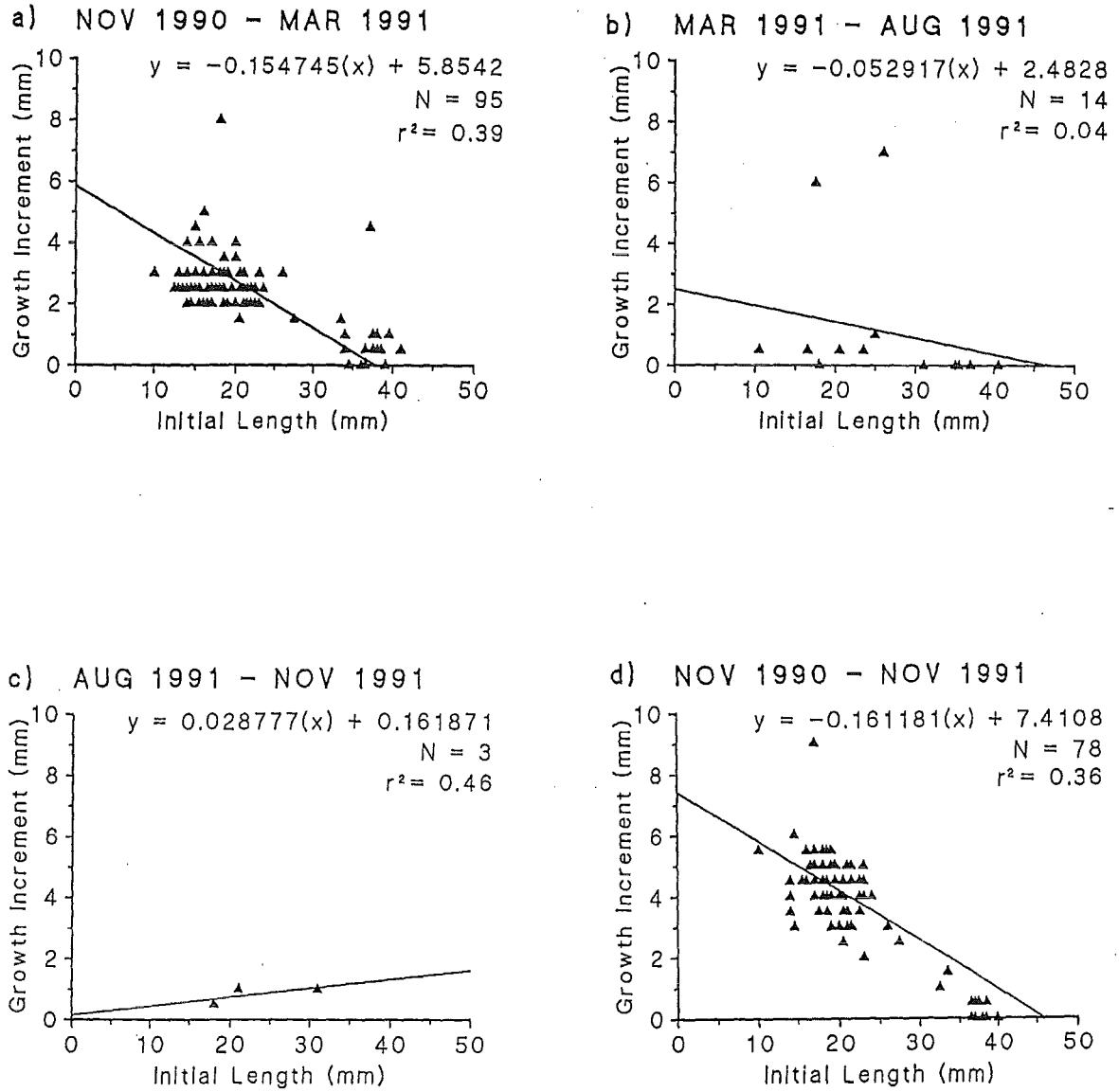


Figure 4.5 Growth increment versus initial shell length from tag-recapture data at Whakatu Point for: **a)** November 1990-March 1991 **b)** March-August 1991 **c)** August-November 1991 **d)** November 1990-November 1991.

Analysis of covariance indicated that the slopes of growth increment versus initial size differed significantly between Spaniards Bay and Whakatu Point during the November 1990-November 1991 and November 1990-March 1991 recapture periods **(Table 4.1)**. The March-August 1991 data could not be tested because the variances of the regression slopes were unequal, and the Whakatu Point slope was insignificant ($F_{1,12}$ = 0.47). Similarly the August-November 1991 regression slopes could not be tested because the number of animals recaptured at both Spaniards Bay (n=4) and Whakatu Point (n=3) during this period were too small.

Table 4.2 Covariance analysis on the relationship of increment vs. initial size at Spaniards Bay and Whakatu Point. Variances were equal and this ANCOVA R is a test of slopes: **a)** full year, November 1990-November 1991, and **b)** period of greatest growth, November 1990-March 1991.

SEASON TESTED	F VALUE	P VALUE	SIGNIFICANCE
Nov 90-Nov 91	$24.61_{1,67}$	3.9201	Different (P < 0.01)
Nov 90-Mar 91	$94.97_{1,182}$	3.8415	Different (P < 0.01)

Growth rates during the period of greatest growth, November 1990-March 1991, were greater at Spaniards Bay than at Whakatu Point. *Turbo* with initial shell lengths of 20mm would be expected to grow 4.5mm at Spaniards Bay and 3.0mm at Whakatu Point between November 1990-November 1991.

Von Bertalanffy plots of shell length against age show decreasing growth rates with increasing age at both sites **(Figure 4.6)**. The growth coefficient (K) and asymptotic length ($L\infty$) at Spaniards Bay are greater than at Whakatu Point **(Table 4.2)**. Sizes at age differ between Spaniards Bay and Whakatu Point. For example an animal of

shell length 30mm is expected to be 4 years of age at Spaniards Bay and 6 years at Whakatu Point.

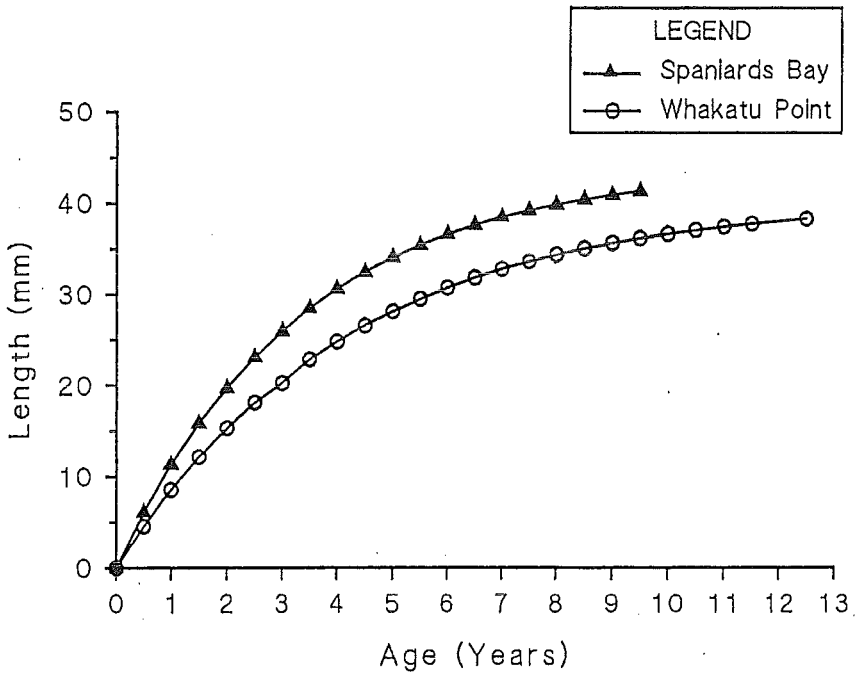


Figure 4.6 Von Bertalanffy growth curves as derived from tag-recapture data for Spaniards Bay and Whakatu Point.

Table 4.3 Growth parameters for Spaniards Bay and Whakatu Point as estimated by the von Bertalanffy growth model. K = growth coefficient and L_∞ = asymptotic length.

Site	K	L_∞
Spaniards	0.299	43.87
Whakatu	0.239	40.33

4.3.3 Expected Year Classes (Modes).

Expected modes as derived from length-frequency and tag-recapture data occur at smaller shell lengths at Whakatu Point than at Spaniards Bay **(Table 4.3)**. Although no distinct modes occurred between shell lengths of 14-21mm in the January 1992 Whakatu Point length-frequency histograms, one is expected to occur at 14mm and another at 19mm. Expected modes predict that the second distinct mode in Spaniards Bay January length-frequency histogram is comprised of two year classes, one at shell length of 22mm and the other at 26mm.

Table 4.4. Expected year classes (modes) as estimated from annual growth increment linear regression growth plots.

Year Class	Spaniards	Whakatu
First mode	12.0-15.0	8.0-14.0
2	20.5-23.0	14.0-19.0
3	26.5-28.0	19.0-23.5
4	31.0-31.5	23.5-27.0
5	33.5-34.0	27.0-30.0
6	35.5-36.0	30.0-32.5
7	37.5-38.0	32.5-35.0
8	38.0-38.5	35.0-37.0
9	---	37.0-38.0
10	---	38.0-39.0
11	---	39.0-40.0

4.3.4 Mortality

It is likely that mortality was not accurately estimated from the number of recaptured tagged *Turbo* at either Spaniards Bay or Whakatu Point. The number of non-recaptured animals a year after release would not accurately estimate mortality rates in *Turbo* populations because:

a) A high rate of paper tag loss was observed in laboratory conditions. Conditions in the field are harsher than those in the labortory, so presumably substantial tag loss of this type of tag occurred in the field.

b) Empty tagged shells may have moved large distances or been reduced to small fragments by wave action or predators (Tegner and Butler 1985).

c) *Turbo* are highly mobile, with considerable horizontal movement on a shore (Beckett 1969). Therefore, all animals that were not recaptured are not necessarily mortalities.

The recapture rates of *Turbo* from this study (6.5% at Spanirds Bay and 16% at Whakatu Point) can be considered minimum levels of survival in these populations.

4.4 DISCUSSION

The distinct modes evident in Spaniards Bay and Whakatu Point length-frequency histograms are indicative of years of strong recruitment and/or low mortality rates. Each mode could represent a year class and the difference between modes, annual growth rates if: **a)** spawning and recruitment occur predictably and annually **b)** mortality rates act equally on all age classes and between years. However, comparisons with tag-recapture data to predict expected modes, occurrence of spawning seasons (Chapter Five) and recruitment (Chapter Two) indicate that such assumptions cannot be made for these *Turbo* populations.

Expected modes cannot be assumed to accurately predict the occurrence of modes in length frequency histograms of a population because annual growth increments are based on one year of data collection. Growth may well vary throughout the lifetime of *Turbo* (eg. Pirker 1992).

As predicted by tag-recapture data, year class modes are expected at shell lengths of 15 and 19mm at Whakatu Point. The absence of modes at these points may be indicative of years of recruitment failure. Recruitment failure may result from the failure of breeding stock to spawn, high mortality of *Turbo* larvae in the plankton, failure of water currents to carry larvae to that site and high mortality of settlers on the shore as a result of predation or unsuitable physical factors (Underwood 1979).

Comparison of expected and actual modes allows interpretation of modes which may represent more than one age class. Expected modes suggest that two age classes occurred in the second cohort of Spaniards Bay January 1992 length-frequency histogram. Separate age classes may merge into one mode because of variability in growth rates between years, and the presence of individuals with growth rates significantly higher than the mean for a particular age class. Slower growth in the first year, perhaps caused by factors such as the unavailability of food, would allow subsequent year classes which may be growing at faster rates, to merge with it. Mortality and slower growth rates at larger sizes also cause modes to become less distinguishable.

The use of linear regressions fitted to annual growth increment and initial length data to estimate von Bertalanffy parameters, is based on the assumption that overall growth rates in each population do not vary between years. However, external factors such as food availability and temperatures may cause variation to occur in overall growth rates of a population between years. Because estimated modes are derived from one year of growth tagging data, the accuracy of where age class modes are expected to occur may not be representative of growth over the lifetime of *Turbo*.

Growth rates of *Turbo* at Spaniards Bay and Whakatu Point decrease with increasing size. This is supported by the coalescence of modes with increasing shell length on length-frequency histograms, negative gradients of linear regressions fitted to growth increment/initial length data and decreasing slope of von Bertalanffy curves with increasing age. *Turbo* populations on Echinoderm Reef at Leigh were found to have linear growth for the first three years, decreasing thereafter (Walsby 1977). At Fergusson Wharf Auckland, the population grew up to 10mm in the first year, 6mm in the second and 4-6mm in the third. After 4 years age classes tended to merge. *Turbo* at Fergusson Wharf (Grange 1974), *Cookia sulcata* (Hartley 1978) and *Haliotis iris* (Poore 1972, Sainsbury 1982, Wilson 1987) also exhibit trends of decreasing growth rates with increasing size. Poore (1972), Sainsbury (1982) and Wilson (1987) observed that fecundity increased with increasing size, suggesting that energy may be channelled into reproduction rather than growth at larger sizes.

Grange (1974) determined that the *Turbo* population studied at Fergusson Wharf in Auckland consisted of at least 5 separate year classes. It appears that *Turbo* populations at Spaniards Bay and Whakatu Point consist of more than seven year classes. A *Turbo* with a shell length of 40mm will be 10 years of age at Spaniards Bay and 13 years at Whakatu Point. However, the von Bertalanffy growth model **a)** obscures the effects of variation in individual growth, and **b)** assumes no selective mortality by size within year classes (Ricker 1975). Therefore, individuals of a particular size may not be the age predicted by the von Bertalanffy growth model, but **a)** be individuals with growth rates significantly above the mean growth rates for a particular age class, or **b)** have emigrated from areas of faster growth. The accuracy

of predictions of size at age from the von Bertalanffy growth curve is also subject to error because they are derived from only one year of sampling, when it is known that growth rates do vary annually (Pirker 1992).

Growth rates of *Turbo* vary spatially as demonstrated by both size-frequency and tag-recapture techniques. Spatial variability of growth rates also occurs between populations of other species of marine gastropods (Leighton and Boolootian 1963, Poore 1972, Shepherd and Laws 1974, Sainsbury 1982). Shepherd *et al* 1983 suggest that spatial variability in growth rates may result from differences in food availability arising from small scale differences in habitat. The faster growth rates of *Haliotis rubra* in areas of greater exposure is a result of the rougher water churning up seaweed beds creating drift algae, which is the principle food of abalone (Shepherd *et al* 1974, McShane *et al* 1988). The faster growth rates that occurred at Spaniards Bay 1990/1991 could also be relate to exposure, because the mid and outer regions of Spaniards Bay are exposed to harsher wave action than occurs at Whakatu Point (Rasmussen 1965).

Growth rates of *Turbo* vary seasonally. At both Spaniards Bay and Whakatu Point, growth rates are greatest during summer months. Similar seasonality of growth rates occurs in *Haliotis iris* (Poore 1972, Sainsbury 1982, Wilson 1984) and other Haliotid species (Leighton *et al* 1963, Shepherd *et al* 1974), although no seasonality was found in the growth rates of the subtidal Turbinidae, *Cookia sulcata* at Leigh (Hartley 1978). Slower growth rates of abalone over winter months could be attributed to the channelling of energy into gonadal production (Shepherd *et al* 1983).

The reasons for temporal and spatial variability of growth rates relate, to some extent, to the variability of external factors which determine growth rates. The occurrence of such variability over short distances highlights the need to determine growth rates at more than one site, for more than one year, preferably using more than one method. The trend of decreasing growth rate with increasing size indicates the need to sample growth rates over a wide range of sizes. A bias of large animals is likely to underestimate the overall growth rates for the entire population, and *vice versa* if only

smaller animals are used to determine growth rates. Maller et al (1988), in demonstrating the asymptotic unreliability of the Fabens method of fitting the von Bertalanffy curve to capture recapture data, similarly recommended that the ages at release should be distributed over a wide interval and should cover the period of most rapid growth, and the recapture times should be large and well distributed over a wide interval.

The occurrence of year classes at any one site and their respective growth rates do not act independently of the population dynamics of the species. Growth rates are temporally and spatially variable, being influenced by the timing and success of reproductive effort, the variability of external conditions influencing survivorship and occurrence of planktotrophic larvae, settlers, recruits and adults of a population. Therefore, to determine comprehensively the growth rates of a population, mortality rates, recruitment and trends in reproductive cycles need to be determined also.

CHAPTER FIVE

REPRODUCTIVE BIOLOGY

5.1 INTRODUCTION

The investigation of a species' reproductive biology is essential in understanding of its ecology. Various methods suitable for the study of marine invertebrates have been developed.

Gonad index techniques are used to describe annual trends in reproductive cycles. The index is a ratio, usually expressed as a percentage, of gonad size relative to body size (Giese 1959). A ratio of dry gonad weight to dry body weight was used by Gonor (1972) and Grange (1974). Boolootian *et al* (1962, cited in Grange 1974), Poore (1973), Shepherd and Laws (1974), Sainsbury (1982) and Wilson (1987) examined cross sectional areas of the gonad and Loosanoff (1965, cited in Grange 1974), the thickness of gonadal tissue.

When plotted as a function of time, gonad indices can be used to determine spawning periods. Under the assumption that an immature or spent gonad is small (Giese 1959), a sudden decrease in the gonad index may be indicative of spawning. The disadvantages of using gonad indices to describe trends in a reproductive cycle are: **a)** There is little information on the amount of tissue other than gametes in the gonad **b)** Time at which gametogenesis was initiated post-spawning is not indicated (Webber and Giese 1969). For these reasons other techniques may be used in conjunction with gonad index methods.

Development of gametes can be studied microscopically from stained sections of the gonad tissue mounted on slides (Webber and Giese 1969, Underwood 1972, Grange 1974, Wilson 1987). Underwood (1974) plotted the number of mature and immature oocytes in sections as a function of time, while Dinamani (1974) and Orton *et al* (1956,

cited in Grange 1974) classified gametes into developmental stages. The quantity of each stage present in the gonad at any time can be used to determine sexual maturation, the onset of gametogenesis and spawning. When used in conjunction with gonad indices, histological examination of gonads is thought to be a reliable indicator of reproductive activity.

Estimates of fecundity, when combined with size frequency distribution data, are useful in determining egg-per-recruit models, the size at onset of maturity, and the proportion of mature animals over a size range (Annala *et al* 1987). The number of oocytes can be estimated by direct subsampling from the ovary (Wilson 1987), or from those which have been released into seawater (Grange 1974).

The sex ratio of a population can be indicative of differential mortality of one gender. Sex ratios have been determined for *Haliotis* species using data collected during investigation of trends in reproductive cycles (Poore 1973, Wilson 1987). Walsby (cited in Grange (1974) as a personal communication) found *Turbo smaragdus* at Echinoderm Reef, Leigh to have a 1:1 sex ratio.

Turbo are known to be broadcast spawners (Grange 1974) and have a primitive reproductive system. Gametes pass from the gonad through the right nephridium into the mantle cavity from which they are released into the water column for fertilisation and subsequent development (Barnes 1987).

This study sought to investigate the reproductive biology of *Turbo*, thereby furthering the understanding of its ecology, and in particular, to determine spawning periods and subsequent recruitment. Gonadal indices and histological techniques were employed to assess trends in an annual reproductive cycle, so that spawning seasons, gametogenesis, fecundity, sex ratio and size at sexual maturation could be determined.

5.2 MATERIALS AND METHODS

Qualitative and quantitative methods were used to describe trends in the annual reproductive cycle of *Turbo* from Lab Rocks on the Kaikoura Peninsula. Qualitative analysis of slides prepared from sections of *Turbo* gonads enabled gonad structure, types of gamete and gonad condition to be defined, whereas quantitative methods measured the changes in gonad composition throughout a reproductive cycle. Other techniques were employed to determine fecundity and size at sexual maturation.

5.2.1 Gonad Indices

Twenty *Turbo* with shell lengths of 35-40mm were collected at monthly intervals from February 1991-April 1992 from Lab Rocks. Preliminary investigations indicated that Turbo of this size range have attained sexual maturity, and were abundant at the sampling site. A narrow size range was selected to reduce variability in the data resulting which could be caused by gonad size increasing with increasing size of the animal (Gonor 1972). Each animal was removed intact from its shell and operculum, sexed and the gonad dissected from the body. Body tissue and gonad were placed in a watchglass and left at room temperature for 24 hours, followed by 24 hours in a thermowave oven at 70°C. Total dry body tissue and dry gonad weight were measured to 0.0001gms.

The gonad index of each specimen was calculated using the formula:

$$\text{Gonad Index} = \frac{\text{Dry Gonad Weight} \times 100}{\text{Total Dry Tissue Weight}}$$

(Gonor 1972).

For each sex, the mean gonad index, with standard errors, was plotted against time.

To determine if gonad index and gonad size increases relative to body size, (as observed by Gonor, 1972), a stratified sample of 57 *Turbo* was collected from Lab

Rocks in July 1991, as part of Chapter Three (Morphometric Relationships). Gonad indices of sexually mature individuals were determined using the method described above. Gonad indices for both sexes was graphed against shell length (measured to the nearest 0.5mm), as were the wet weights of the dissected gonads (measured to the nearest 0.001mm).

5.2.2 Qualitative Analysis of Gonad Composition.

At monthly intervals 30 *Turbo* of assorted sizes were collected from Laboratory Rocks between January 1991-February 1992. Following the recommendation of Underwood (1972) and Grange (1974) the animals were retained in running seawater in the laboratory without food for two days, thereby, allowing the food particles that could otherwise cause difficulties when sectioning to be expelled from the digestive gland. Shell length was measured to the nearest 0.5mm and the body tissue was removed. Gonad and digestive gland were dissected from the visceral mass and placed into individually labelled containers of Bouins solution for fixation and storage. 5mm sections were dissected from the mid-region of the gonad, placed into labelled baskets and stored in 70% alcohol. Samples were embedded in paraffin wax and slides prepared and stained using Ehrlich's haematoxylin and eosin.[1]

Slides were qualitatively analyzed to determine and define: **a)** gonad structure of female and male *Turbo*, **b)** gamete type and stages of development, **c)** the phases of gonad condition, as the composition of gametes and associated material varies through an annual reproductive cycle.

Data are presented in a descriptive form, using structural and developmental information of the reproductive systems of similar species, to interpret and compare with those described here for *Turbo.* In this manner, qualitative analysis provided background data of gonad structure and composition for further quantitative analysis of gonadal development throughout a reproductive cycle.

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[1] For further information pertaining to the methods used to prepare histological slides from the samples please refer to Appendix V.

5.2.3 Quantitative Analysis of Gonad Composition

The histological slides that were prepared from sections of *Turbo* gonads[2] and qualitative descriptions of gametes and stages of gonad condition from Section 5.2.2, used to quantatively analyze changes in the composition of the gonads throughout a reproductive cycle.

For each monthly sample of *Turbo*, five sections of each sex, from individuals of shell lengths 35-40mm, were sub-sampled to determine quantitatively the changes through time in gamete composition within the ovary and testis. Using results from qualitative observations, categories used to describe material in the ovaries of females were mature oocytes, immature oocytes, oogonia/trabeculae and extra-cellular matrix. The testes of males were categorised as having spermatozoa, spermatocytes, spermatogonia/trabeculae and extra-cellular matrix.

A point-count method was used to estimate the gonad composition from the histological sections. A grid, with intersections regularly spaced 0.09mm apart was placed in the eye piece of a compound microscope. The intersections used in each sample were determined by a random number generator that selected the initial intersection, from which a further 14 intersections were counted off in a direct line. The category of material type beneath the 15 intersections of the grid was noted. Five sub-samples from each of the ten slides were taken in this manner. Composition of the gonad was calculated as relative density (%) of each category type. The mean monthly density (%) for each category was plotted with standard errors as a function of time.

The thickness of the walls of the gonads was estimated using a micrometer that was placed in the eye-piece of a compound microscope. The micrometer was positioned perpendicular to the wall of the gonad, and the total wall width (outer epithelium and muscle layer inclusive) measured to the nearest 0.001mm. Five random sub-samples

[2] The methods used to collect samples and prepare the histological slides of sections of the gonads are described in section 5.2.2 and Appendix V.

from each individual were conducted in this way. The mean monthly wall thickness was plotted, with standard errors, as a function of time.

5.2.4 Fecundity

Fecundity, as defined here, is the number of oocytes in an ovary immediately prior to spawning. No differentiation was made between physiologically mature and immature oocytes.

On 9 January 1992, when gonads were ripe, a stratified sample of *Turbo* was collected from Lab Rocks, selecting five females for each 5mm size class greater than 20mm (n = 20). Shell lengths were measured to the nearest 0.5mm. The gonad and associated digestive gland of each *Turbo* were removed and placed in 10% formalin to harden overnight. The gonad was then dissected from the digestive gland and weighed to the nearest 0.001gm. A smaller sample was dissected from the mid region of the gonad, weighed to the nearest 0.001gm and placed in a jar containing 30ml of distilled water. Oocytes were loosened from the ovary membrane and trabeculae by vigorous shaking and a sharp probe was used to separate remaining oocyte clumps. Five 0.25ml sub-samples of each individual were extracted with a pipette and examined at 60x magnification using a binocular microscope to count the number of oocytes. Knowing the mean egg count and the proportion of ovary weight to sub-sample weight allowed an estimation of total oocyte number. This was plotted against shell length and a curve fitted.

5.2.5 Sex Ratio

Sex ratio was estimated by using the slides prepared from the gonads of *Turbo* collected between January 1991-January 1992 (in section 5.2.2; n = 332). The sex was determined by examination of the gametes in the gonad at 125x magnification. Frequency of sexes was tested against the hypothesis of a one to one ratio, using a Chi-squared test for goodness of fit (Sokal and Rohlf, 1981).

5.2.6 Size at Sexual Maturation

A sexually mature individual, as defined here, was one in which mature oocytes or spermatozoa occurred in the gonad. This is not an indication of the individual's ability to spawn, and does not identify the physiological maturation of the gametes.

All slides from October 1991-January 1992 (n = 113) were examined for the presence of mature oocytes or spermatozoa, thereby determining size at onset of sexual maturation. Gonad index data indicated that gonads were most ripe during these months, therefore lessening the chance of mistaking a gonad depleted from spawning for an immature individual.

5.3 RESULTS

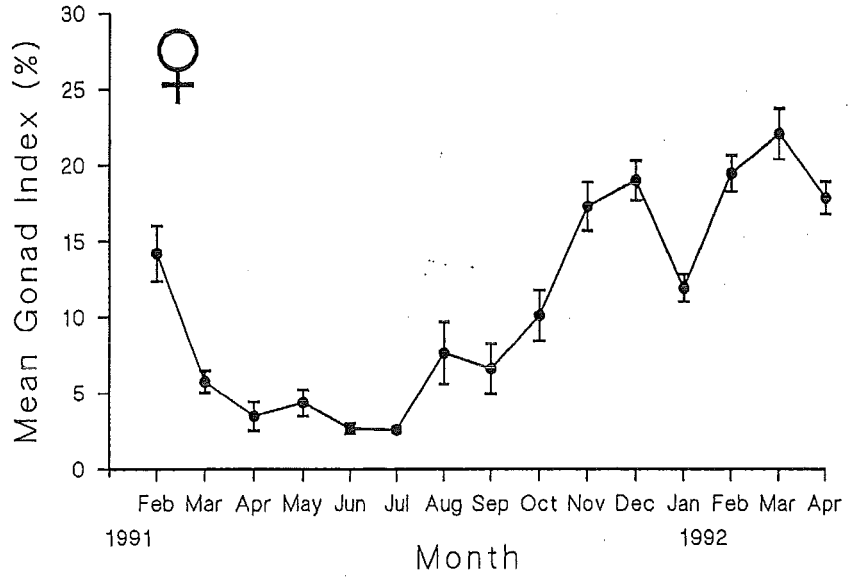
5.3.1 Gonad Index

Clear peaks in the gonad index were evident for both male and female *Turbo* between February 1991-April 1992 **(Figure 5.1)**. The female index decreased from 14.2% in February 1991 to 5.8% in March 1991, and to 3.5% by April. Males showed similar percentage decreases during the same period. Values remained low for both sexes from April until August/September when indices began to increase, peaking in December at 19.0% for females and 18.1% for males. In January 1992, indices dipped sharply to 11.9% for females and 11.4% in males. In contrast to the previous year, indices for both sexes remained high during February-April 1992. For example, during March 1992 the index for females was 22.1% and 19.3% in males, compared to 5.8% and 4.6% the previous year.

Throughout the sampling period, mean monthly gonad indices were similar for females and males, reflecting the synchronisation of reproductive cycles between the sexes.

Gonad indices for both female and male *Turbo* at Lab Rocks increased with increasing shell length **(Figure 5.2)**. However, both sexes exhibited weak correlations ($r^2 = 0.38$ for both females and males), indicating considerable variation in gonad indices between individuals. Similarly, wet gonad weight increases exponentially with increasing shell length **(Figure 5.3)**, although with higher correlation values than those for gonad indices ($r^2 = 0.71$ and males $r^2 = 0.77$).

a)



b)

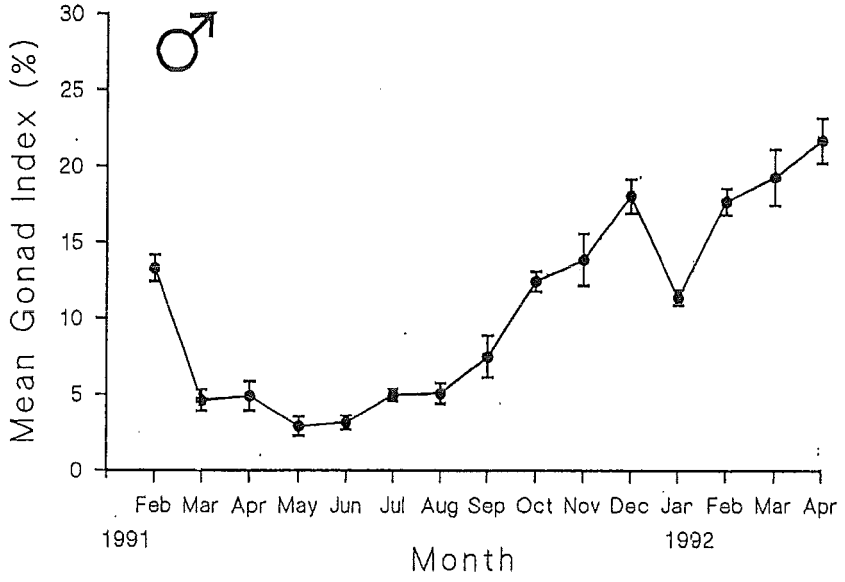
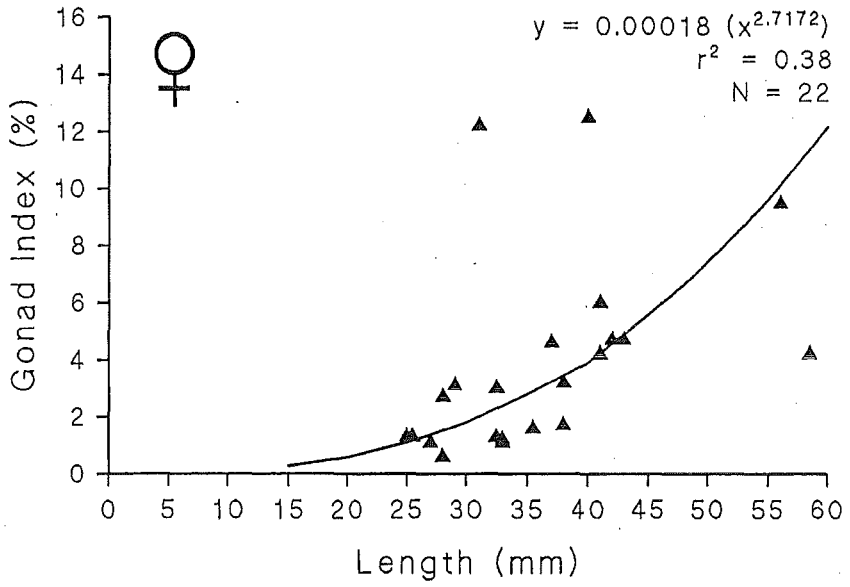


Figure 5.1 Mean monthly gonad indices of *Turbo* between February 1991-April 1992 **a)** females **b)** males. Error bars are ± 1 s.e.

a)



b)

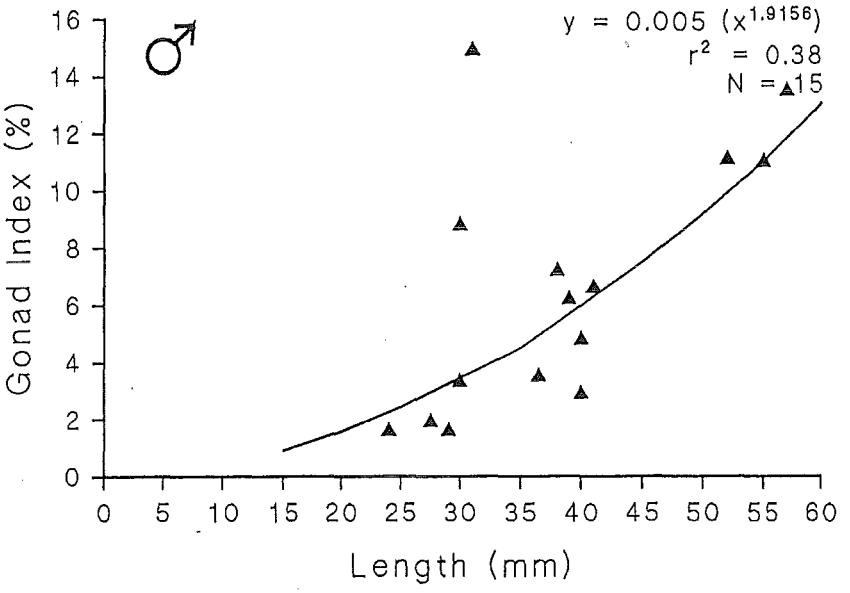
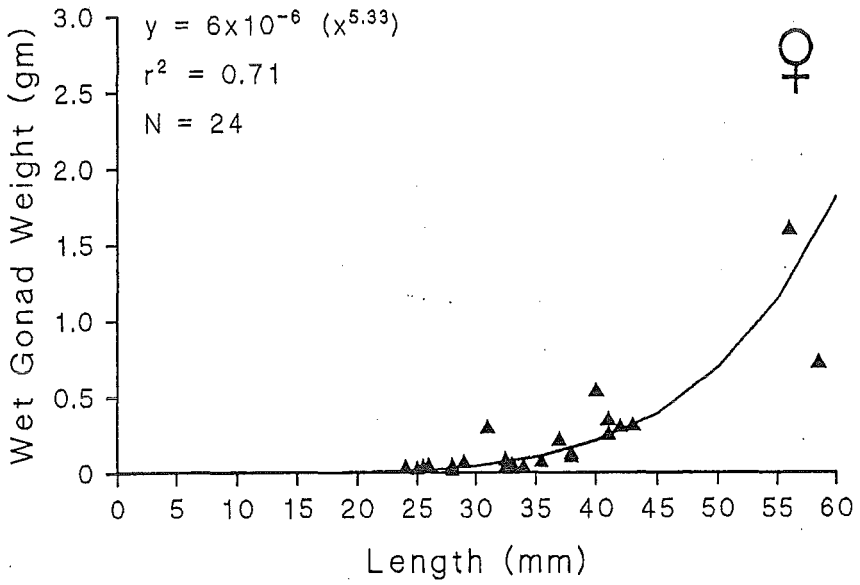


Figure 5.2 Gonad indices against shell length of both **a)** female and **b)** male *Turbo* in July 1991.

a)



b)

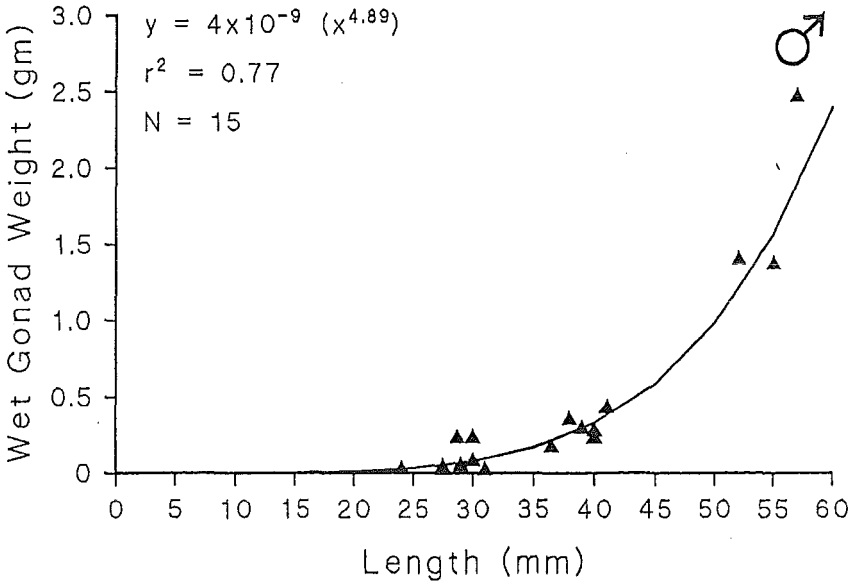


Figure 5.3 Wet gonad weights plotted against shell length for: **a)** female and **b)** male *Turbo* in July 1991.

5.3.2 Qualitative Analysis of Gonad Composition

a) Gonad structure

Turbo are dioecious, each sex having a single gonad which is located in the visceral mass adjacent to the digestive gland **(Figure 5.4)**. Although sex of an individual cannot be determined by viewing the animal externally, it can be distinguished from the colouration of the gonad **(Figure 5.5)**. Female gonads are green, males' are cream and sexually immature gonads are brown and externally indistinguishable from the digestive gland. The colouration is associated with presence of mature gametes, so although evident throughout the reproductive cycle, the colouration is more apparent when the gonad is ripe.

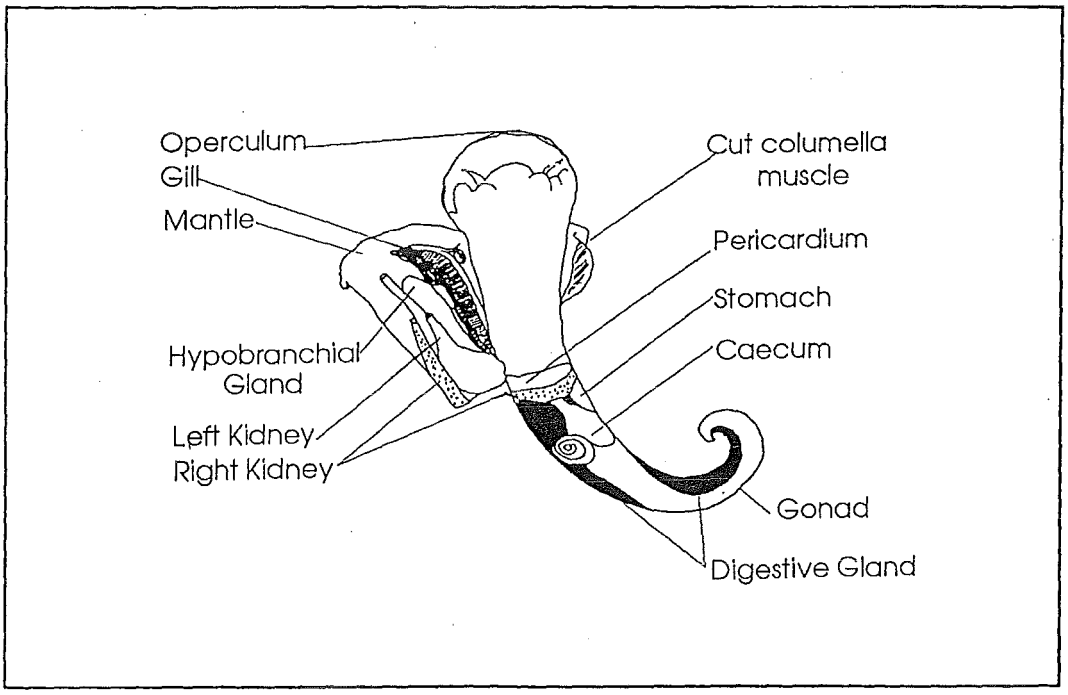


Figure 5.4 Schematic representation of a *Turbo* with shell removed and dissected.

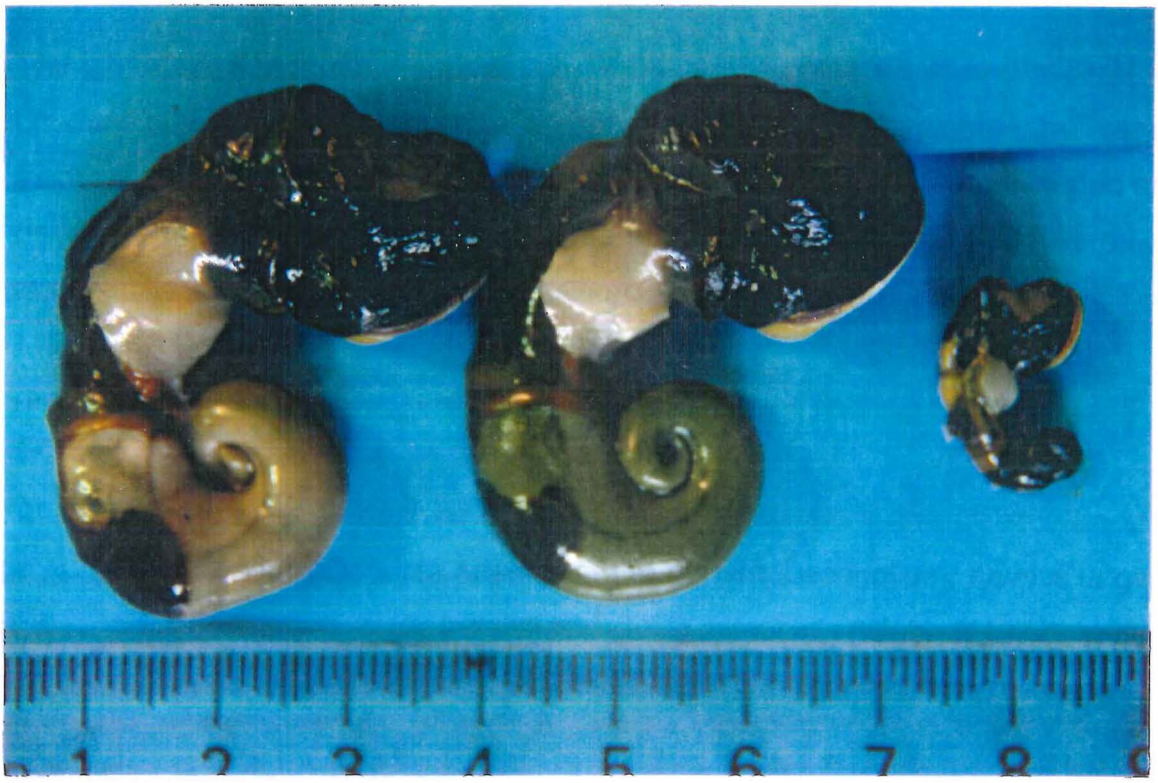


Figure 5.5 *Turbo* removed from the shell showing colouration of the gonad. In sexually mature *Turbo* the gonad of the male **(left)** is cream and green in the female **(middle)**. The gonad of sexually immature *Turbo* appear brown and is externally indistinguishable from the digestive gland **(right)**.

The gonad is enveloped by a wall composed of two layers, an outer epithelium and a muscle layer, which are conspicuous when the wall has thickened post-spawning. The epithelium is a thin outer layer in which secretory and non-secretory cells are found (Grange 1974). The muscle layer forms the inner section of the gonad wall and is thicker than the epithelium. Extensions of the muscle layer into the lumen of the gonad form trabeculae that divide the gonad into follicular spaces. It is from the germinal epithelial cells lining the trabeculae that gametic cells are derived (Raven 1961). These are known as oogonia in females and spermatogonia in males.

b) Gamete type and development

The gametes of both male and female *Turbo* can be categorised and separated into different stages as each develops towards maturity. The developmental stages for each respective sex is categorised, listed and described below. Also included are the descriptions of other relevant tissue types that occur in the gonads and were used in quantitative analysis of gonad composition.

-Female

Oogonia are evident as darkly staining nuclei along the trabeculae at 125x magnification. Oogonia arise from the germinal epithelium, have a large clear nucleus that nearly fills the cell and divide mitotically (Webber 1977), multiplying rapidly to increase in number (Raven 1961).

Immature oocytes remain attached to the trabeculae and are those oogonia in which mitotic replication has terminated (Raven 1961) Three phases of growth are exhibited by immature oocytes (Raven 1961).

i/ 'Pre-meiotic phenomena'. This phase is characterised by the occurrence of a regular sequence of processes in the nucleus and weak or barely perceptible growth.

ii/ 'Pre-vitellogenesis'. Yolk is barely formed, the nucleus swells into the germinal vesicle, protoplasm is synthesised resulting in the slow, regular growth of oocytes.

iii/ 'Vitellogenesis'. In this phase the bulk of the yolk is laid down and growth rates of the oocytes increase abruptly to achieve their final stage in a short period.

Throughout their development immature oocytes remain attached to the trabeculae by a stalk and are recognisable by a distinct nucleolus and increasing amounts of vitelline material. Sizes of immature oocytes vary considerably, ranging in diameter between 0.02-0.10mm. As development continues a gelatinous layer forms around the vitelline material and the primary oocyte moves away from the trabeculae.

Mature oocytes are those which have developed a gelatinous layer and lie free in the lumen of the ovary. The diameters of mature oocytes, excluding the gelatinous layer range between 0.10-0.23mm; including the gelatinous layer, they range between 0.15-0.26mm. Although spherical in shape, both gelatinous and vitelline layers can become angular and irregularly shaped when compressed, as occurs prior to spawning **(Figure 5.6)**

-Male

Spermatogonia are evident as darkly staining nuclei along the trabeculae at 125x magnification. Spermatogonia arise from the germinal epithelium and have a large clear nucleus that nearly fills the cell and divides mitotically (Webber 1977).

Spermatocytes are observed as dark dots at 125x magnification that cluster around the trabeculae. Grange (1974), described spermatocytes as similar in size to the head of the spermatozoa (~5μm). There are two phases of spermatocyte growth in which two meiotic divisions occur (Webber 1977).

Spermatozoa are spermatocytes that have undergone spermiogenesis to form a head, middle piece and flagellum (Webber 1977). The spermatozoa are seen as dark purple streaks filling the follicular spaces between the trabeculae and spermatocyte clusters **(Figure 5.7)** at 125x magnification (~40-60μm). Spermatozoa of *Turbo* are typical eupyrene sperm (Grange 1976).

Extra-cellular matrix is a term used here to describe areas in either male or female gonads that are unoccupied by gametes. This includes vacant areas of the gonad, although care was taken to distinguish between spaces created in preparation of the slides, and areas of extra-cellular material.

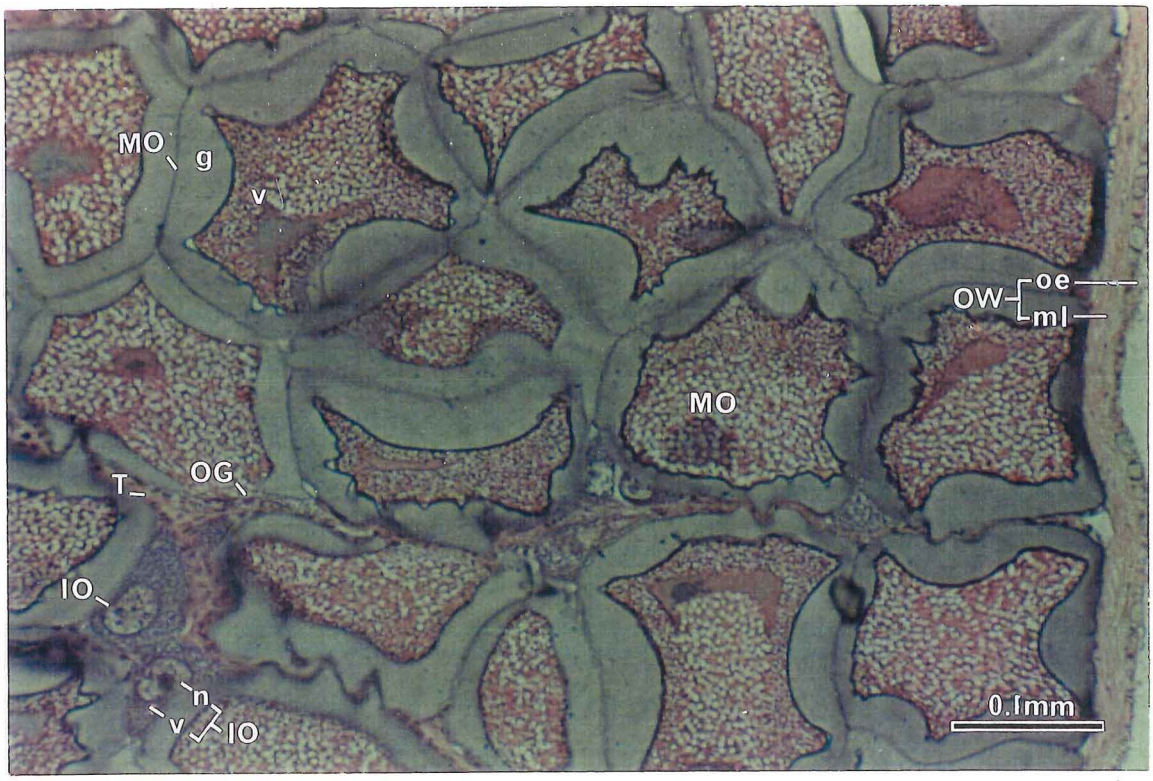


Figure 5.6 A section through an immediate pre-spawn *Turbo* ovary, showing the gelatinous layer (g), and vitelline material (v) of the compressed mature oocytes (MO), trabeculae (T), oogonia (OG) and nucleolus (n) and vitelline material of the immature oocytes (IO).

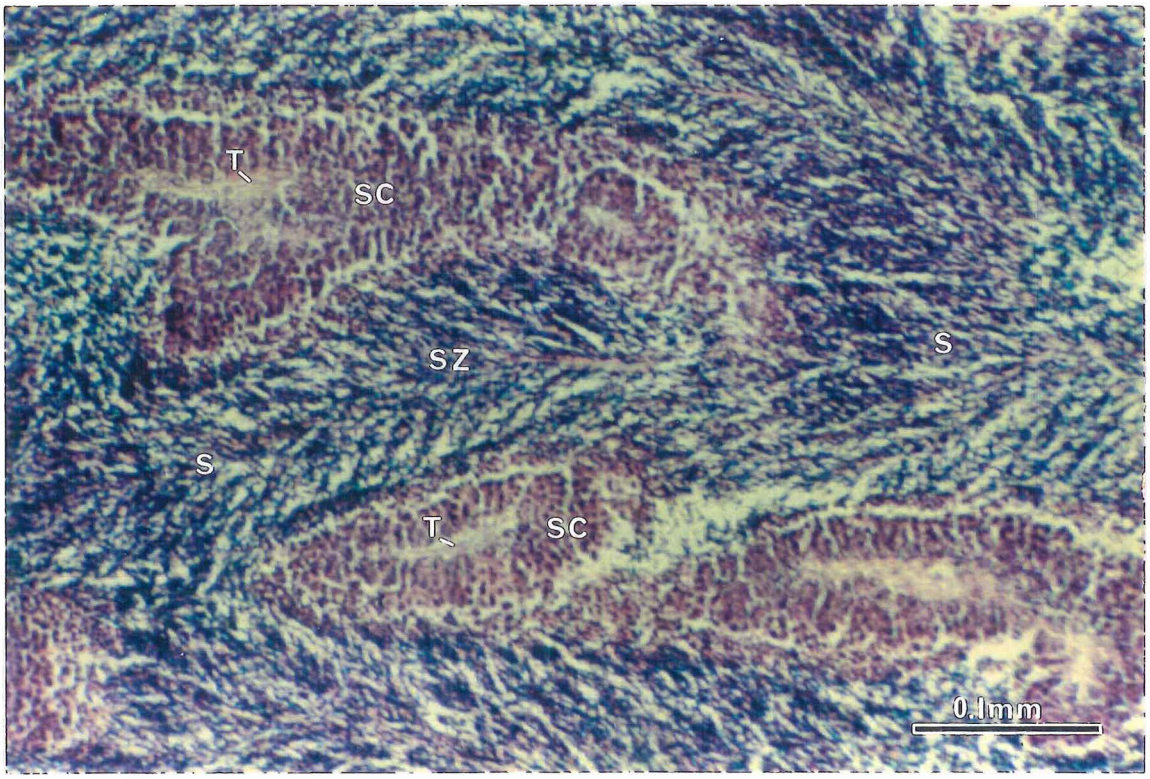


Figure 5.7 A section through an immediate pre-spawn *Turbo* testis, showing spermatozoa (SZ), spermatocytes (SC) and trabeculae (T).

c) Stages of gonad condition

The condition of both female and male *Turbo* gonads varied throughout the annual reproductive cycle of 1991/1992. The changing state of the gonad was classified and into four categories for each sex. Descriptions of sexually immature gonads are included as a comparison to those that are sexually mature.

- Female

i/ Immature

The volume of these gonads, as viewed by transverse sections, is very much less than that for sexually mature individuals. Oogonia are the dominant gamete type in the gonad, although if the individual is close to achieving sexual maturity, small immature oocytes will be present also. No mature oocytes occur.

ii/ Immediate Pre-spawn Phase

Mature oocytes dominate the section **(Figure 5.8)**. The compression of these within the gonads cause distortion of the vitelline material and expansion of the gonad, thereby stretching the ovarian wall. At this stage, the outer epithelium and muscle layer of the inner wall are difficult to differentiate at 125x magnification. Trabeculae are small, more common towards the ovarian wall than towards the digestive gland, and are associated with small clumps of immature oocytes. The immediate pre-spawn phase was observed to occur three months prior to the January 1992 spawning season.

iii/ Immediate Post-Spawn Phase

The ovarian wall is thick, with the outer epithelium and muscle layer easily differentiated at 125x magnification. All stages of gametes are present **(Figure**

5.9). Trabeculae, which are particularly prominent, are speckled with oogonia and small immature oocytes which are attached by stalks. A few mature oocytes, which were not released during spawning, remain. These are spherical and may be tattered and separated from the gelatinous layer, suggesting that reabsorption may be occurring. There are considerable portions of the gonad not occupied by gametes. Instead, they are either empty or filled with a translucent material which could be the deteriorating material of gelatinous layers. Gonad volumes have decreased, as indicated by narrow transverse sections of the ovaries. This stage was observed to occur in individuals in March 1992.

iv/ Mid-Post Spawn Phase.

Trabeculae and associated oogonia are prominent, particularly in the earlier stages of this phase **(Figure 5.10)**, suggesting that gametogenesis occurs within several months of spawning.

Immature oocytes dominate the gonad in number, either attached to the trabeculae by stalks or lying free in the lumen. These are at first small, increasing in size as vitellogenesis proceeds. Vitellogenetic development of the oocytes is slow and constant throughout the winter, increasing abruptly in spring (August/September)

Few mature oocytes other than those that were not released from the ovary during spawning occur in the ovary during the early stages of this phase. However, the numbers of mature oocytes increase abruptly towards the onset of the immediate pre-spawn phase, and are associated with an increase in gonad volume. This was the longest phase observed in the overall condition of the ovary, extending from April-September 1991.

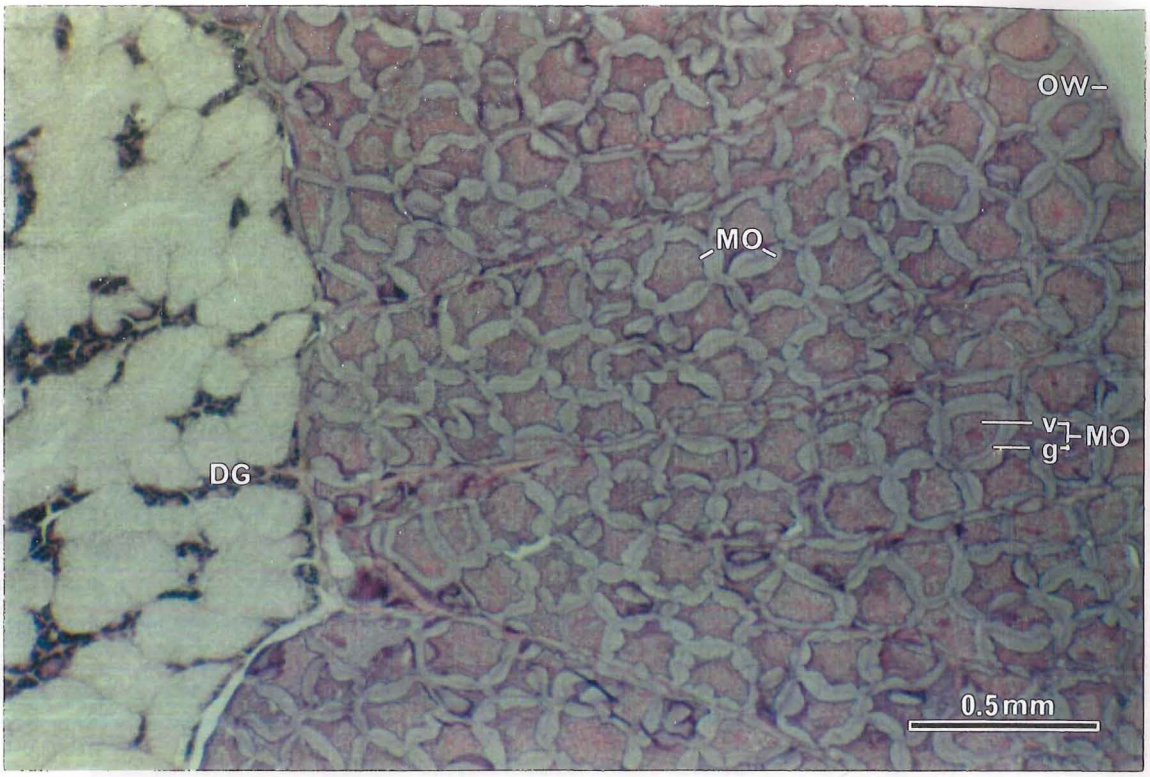


Figure 5.8 A section through an immediate pre-spawn *Turbo* ovary showing mature oocytes (MO), trabeculae (T), ovarian wall (OW) and digestive gland (DG).

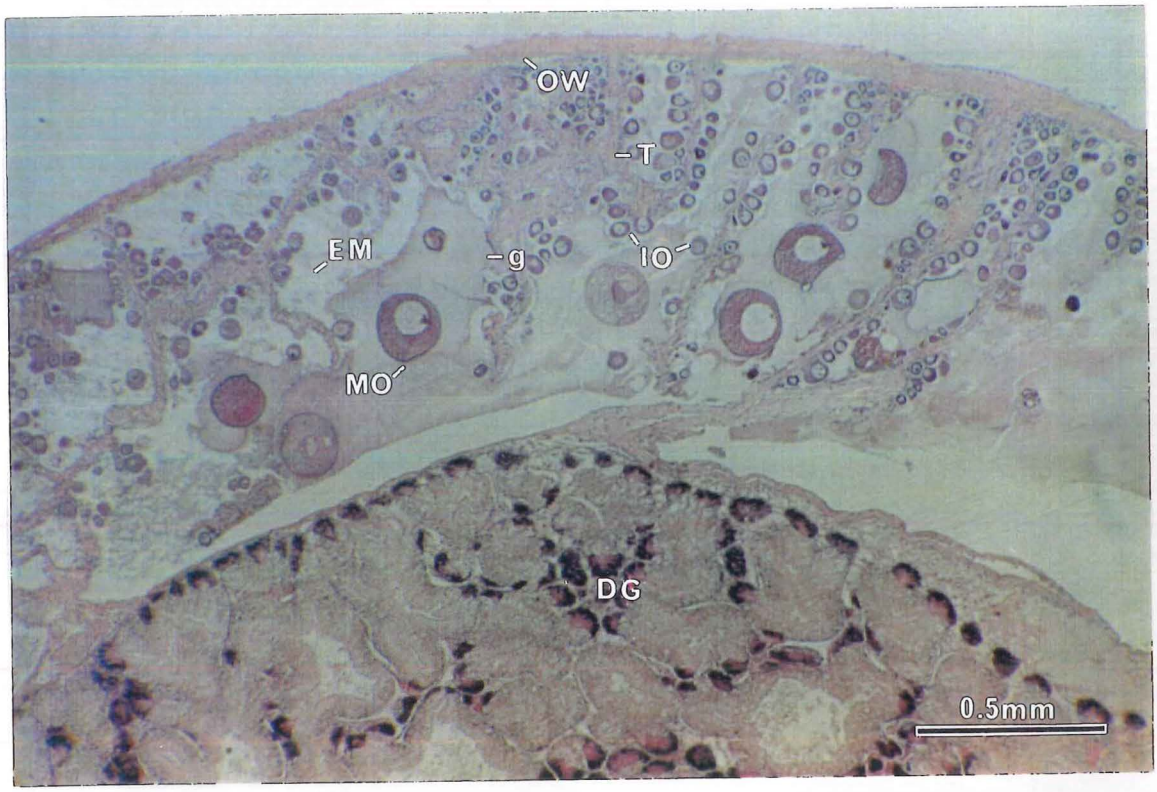


Figure 5.9 A section through an immediate post-spawn *Turbo* ovary showing the dispersed gelatinous layers (g), mature oocytes (MO), immature oocytes (IO), trabeculae (T), ovarian wall (OW), extracellular matrix (EM) and digestive gland (DG).

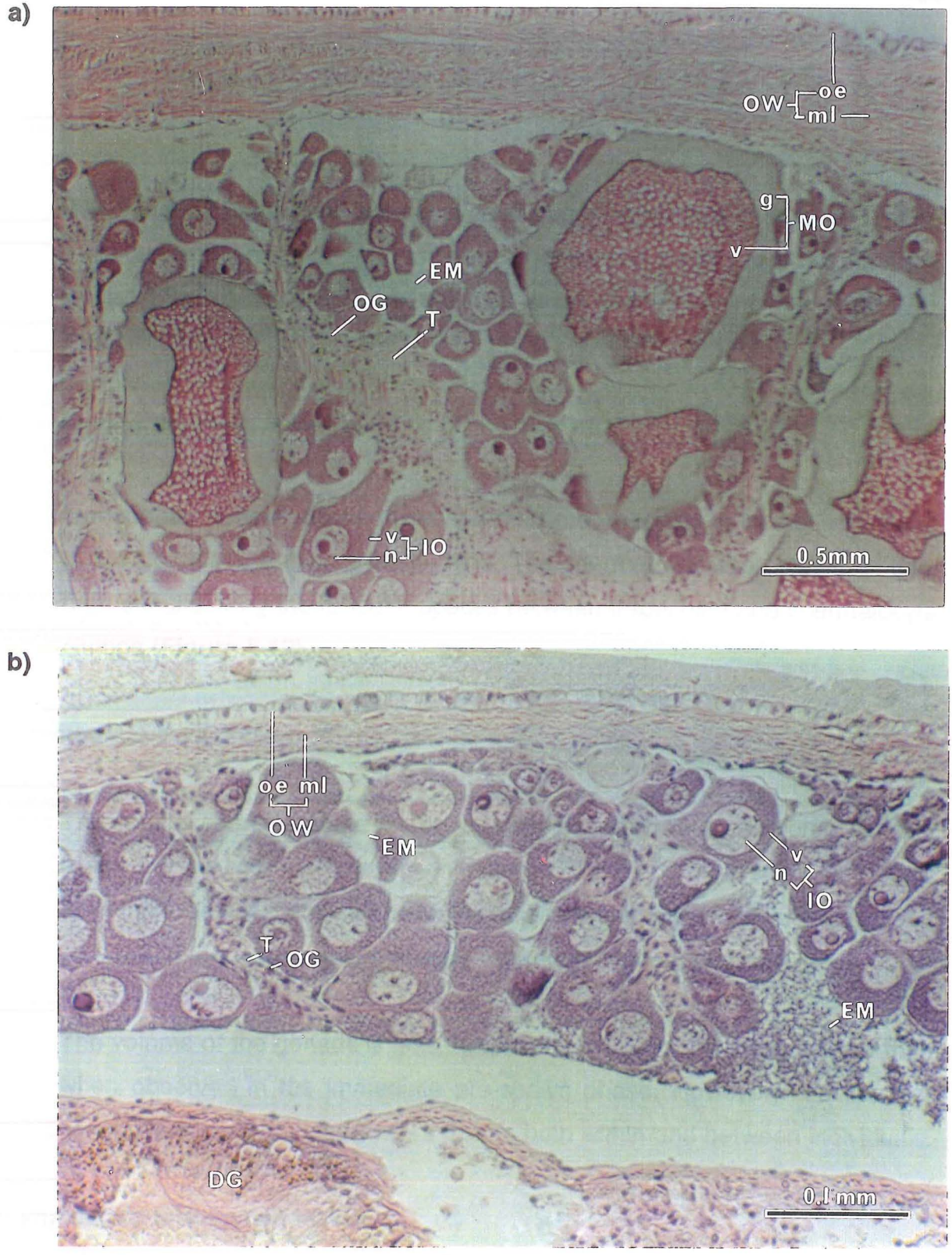


Figure 5.10 Sections through a mid post-spawn *Turbo* ovary showing the gelatinous layer (g) and vitelline material (v) of mature oocytes (MO), the nucleolus (n) and vitelline material of immature oocytes (IO), oogonia (OG), trabeculae (T), outer epithelium (oe) and muscle layer (ml) of the ovarian wall (OW), extra-cellular matrix (EM) and digestive gland (DG) in **a)** April 1991 **b)** July 1991.

-Male

i/ Immature

The volume of immature gonads is small compared to that of sexually mature individuals. Spermatogonia and spermatocytes are dispersed throughout the gonad **(Figure 5.11)** and are seen as small darkly staining nuclei at 125x magnification.

ii/ Immediate Pre-Spawn Phase

Gonads are densely packed with spermatozoa, resulting in increased volume of the gonads and thinner testis walls. The spermatozoa are evident as thin, dark streaks filling the follicular spaces between trabeculae and spermatocyte clumps **(Figure 5.12)**.

iii/ Immediate Post-Spawn Phase

Trabeculae, spermatogonia and spermatocytes are obvious as discrete clumps, to which a few spermatozoa remain attached **(Figure 5.13)**. In some individuals all of the follicular spaces between trabeculae are empty, while in others, some portions of the testis remain densely packed with spermatozoa.

The volume of the gonads is less, and the thickness of the walls greater than when observed in the immediate pre-spawn phase. However, considerable variability of both of these factors occurs both within and between individuals.

iv/ Immediate Mid-Spawn Phase

Follicular spaces between trabeculae are filling and spermatozoa are extending outwards from the trabeculae **(Figure 5.14)**. Part of the gonad may consist of

spermatozoa densely packing spaces between trabeculae, while other areas remain vacuous.

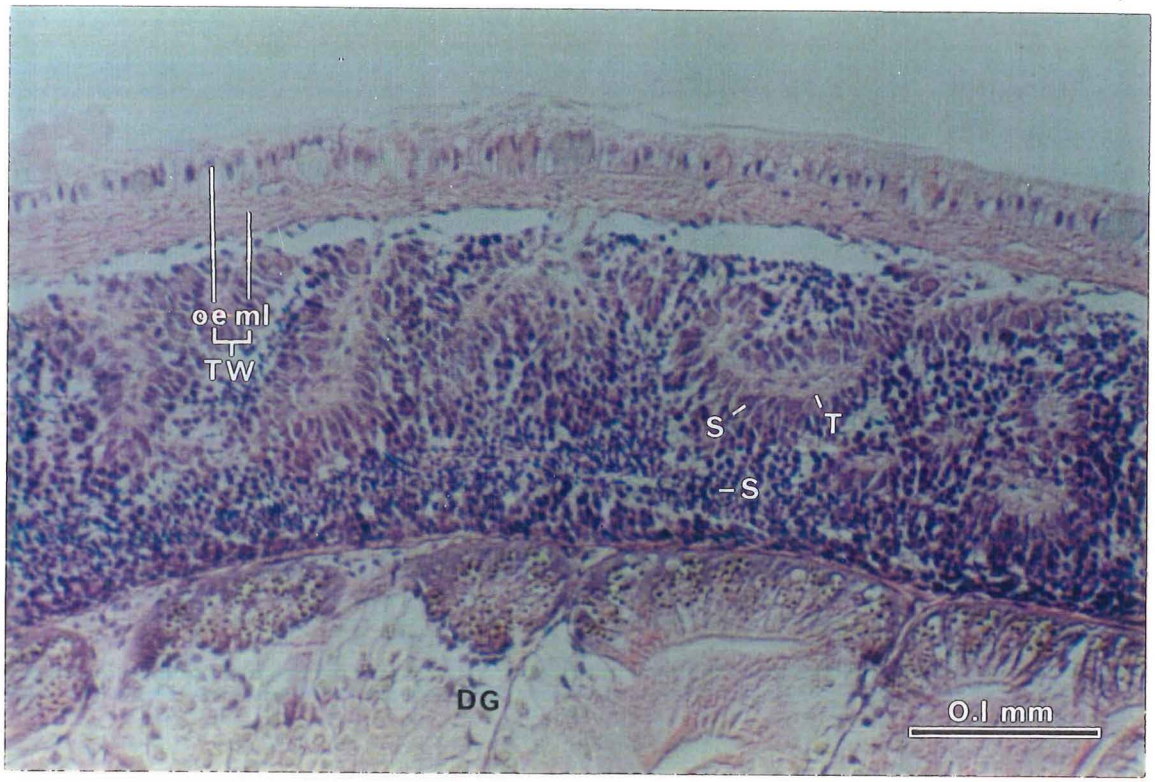


Figure 5.11 A section through an immature *Turbo* testis showing spermatocytes (SC), spermatogonia (SG), trabeculae (T), outer epithelium (oe) and muscle layer (ml) of the testis wall (TW) and digestive gland (DG).

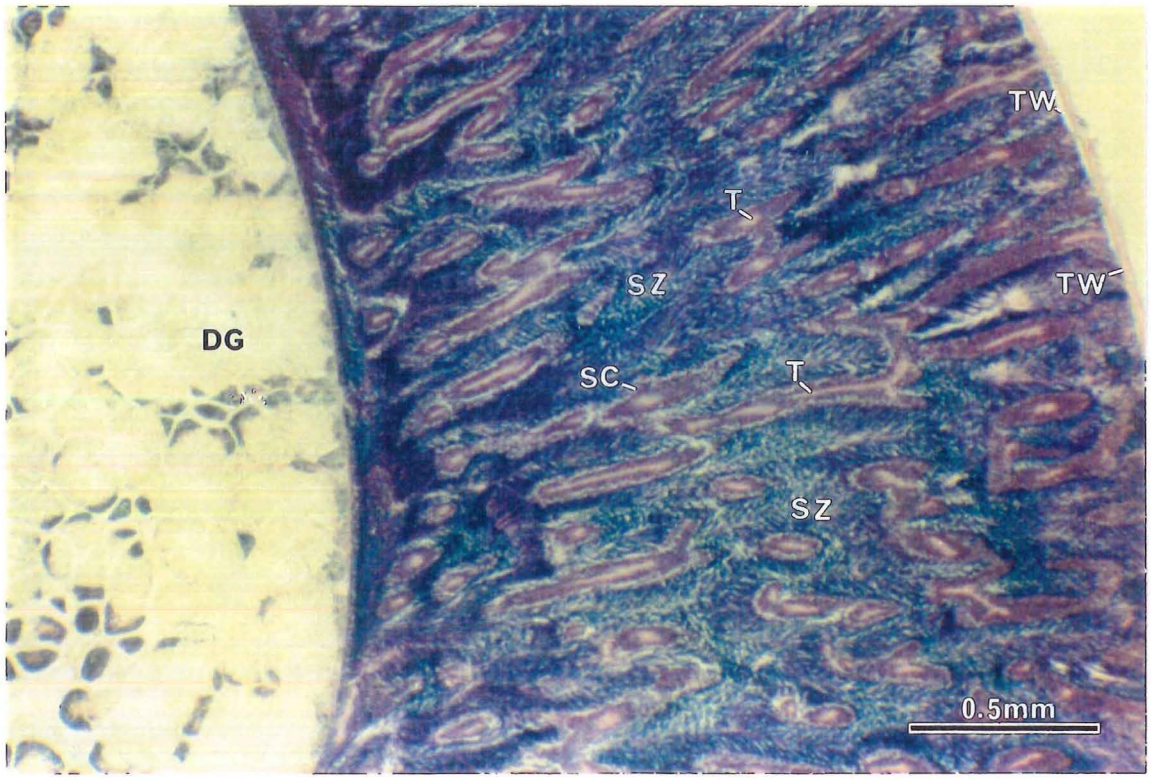


Figure 5.12 A section through an immediate pre-spawn phase *Turbo* testis showing spermatozoa (SZ), spermatocytes (SC), trabeculae (T), testis wall (TW) and digestive gland (DG).

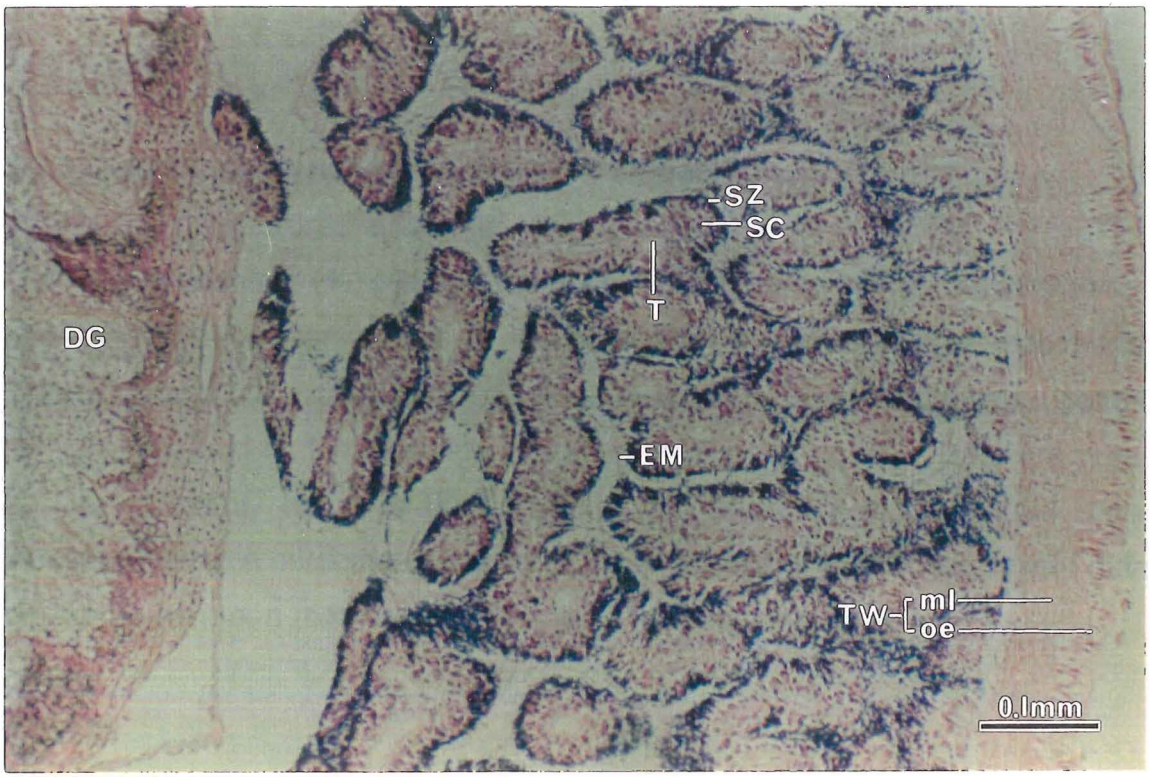


Figure 5.13 A section through an immediate post-spawn *Turbo* testis showing spermatozoa (SZ), spermatocytes (SC), trabeculae (T), outer epithelium (oe) and muscle layer (ml) of the testis wall (TW), digestive gland (DG) and extra-cellular matrix (EM).

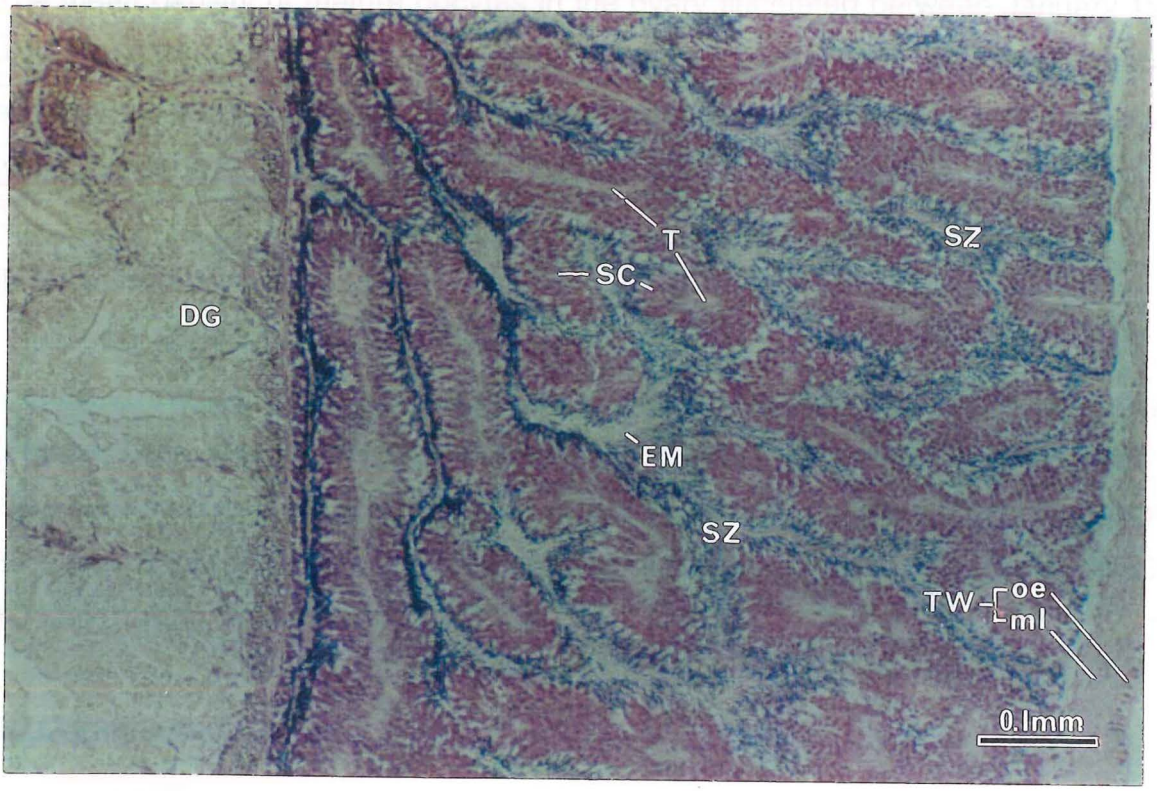


Figure 5.14 A section through an immediate mid-spawn *Turbo* testis showing spermatozoa (SZ), spermatocytes (SC), trabeculae (T), outer epithelium (oe) and muscle layer (ml) of the testis wall (TW) and extra-cellular matrix (EM).

5.3.3 Quantitative Analysis of Gonad Composition

The relative densities (%) of **a)** mature oocytes, immature oocytes, trabeculae/oogonia and the extra-cellular matrix of females and **b)** spermatozoa, spermatocytes, trabeculae and the extracellular matrix of males, were estimated using a point-count sampling method on histologically prepared sections of gonads. Data are presented as mean monthly densities through time. The thickness of the gonad walls was measured using a micrometer placed in the eye piece of a microscope and data also presented as mean monthly wall thickness (mm) against time.

-Female

i/ Mature Oocytes

The mean density of mature oocytes in the ovary fluctuated between January 1991-January 1992 **(Figure 15a)**. Peaking at 97.3% in January 1991, the density dropped abruptly to 34.6% in March 1992 and remained between 40-50% until September, when the density increased rapidly, peaking at 97.3% in December 1991.

ii/ Immature oocytes

Trends in the density of immature oocytes were the converse of mature oocytes **(Figure 15a)**. Oocyte density was less than 2.0% in January-February 1991 but increased notably to 47.8% in March. After this, density declined, fluctuating around 30% until September, after which a marked decrease occurred, with lowest levels of 1.7% occurring in December 1991.

iii/ Oogonia/trabeculae

Oogonia were associated with trabeculae throughout the sampling period, with both oogonia and trabeculae being more abundant during periods of decreased density of mature oocytes **(Figure 5.15b)**. The density of trabeculae increased from negligible

levels in January-February 1991 to a peak of 33.0% in June. A steady decline occurred from 32.7% in September to 1.8% in December.

iv/ Extra-cellular Matrix

Similar trends as those for trabeculae were observed for the extra-cellular matrix in the ovary **(Figure 5.15b)**. Extra-cellular matrix increased from 0.6% in February to 7.2% in March, there after fluctuating around 8.0% until August. The percentage extra-cellular matrix gradually decreased from 4.6% in September to negligible levels in December, at which time the ovaries of sexually mature females were densely packed with mature oocytes.

v/ Thickness of Ovarian Wall

The thickness of the ovarian wall increased with decreasing density of mature oocytes and increasing density of immature oocytes **(Figure 5.15c)**. From a mean wall thickness of 0.016mm in January, the wall thickness increased to 0.065mm in April. A peak of 0.090mm in September corresponded with a peak in relative density of trabeculae during the same period. Similarly, an abrupt dip in December corresponded to peak levels of mature oocyte density in December and low levels of primary oocyte, trabeculae and extra-cellular matrix.

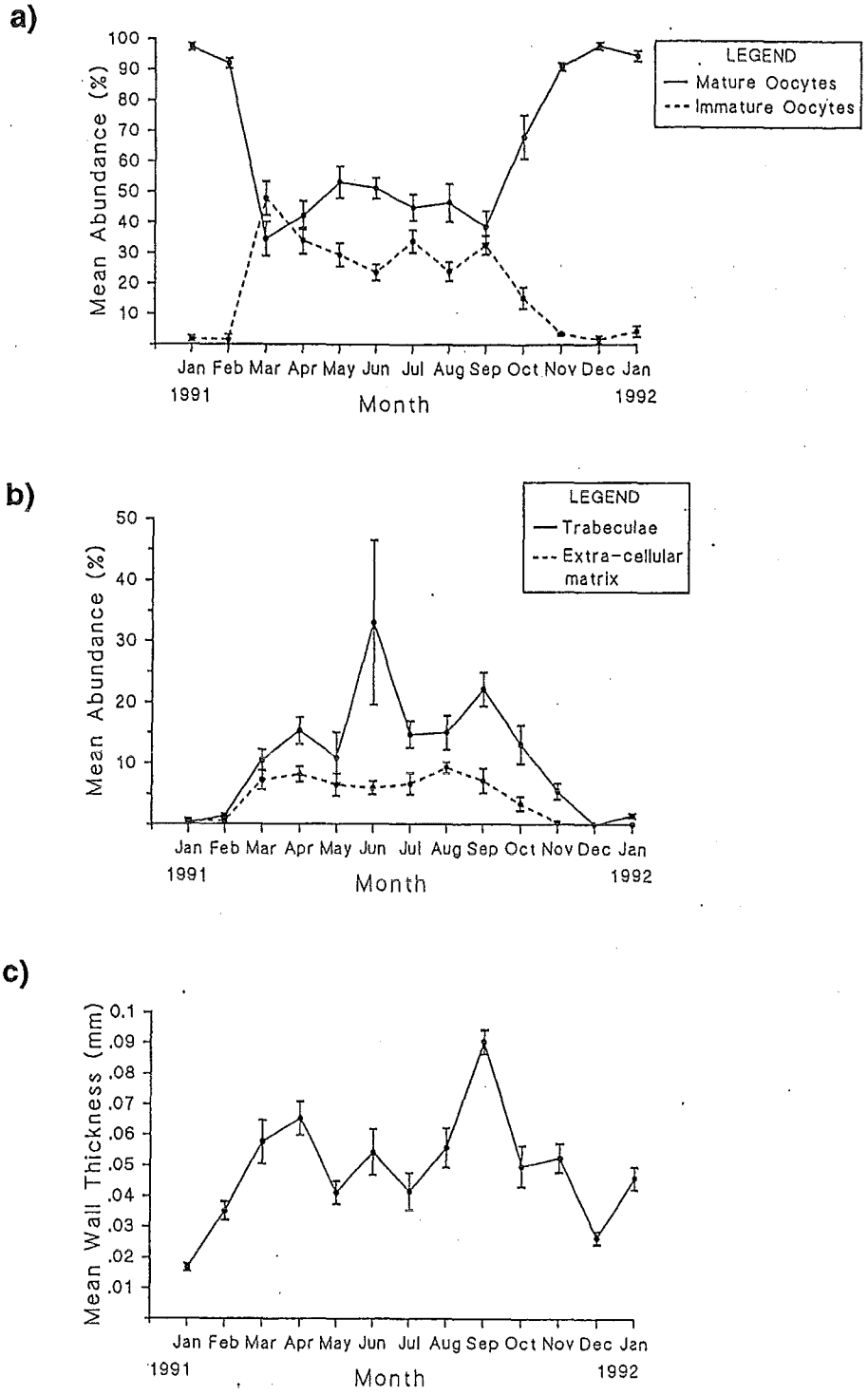


Figure 5.15 Gonad composition of female *Turbo* as described by mean monthly densities between January 1991-January 1992 of **a)** mature oocytes and immature oocytes **b)** trabeculae and extra-cellular matrix **c)** mean ovarian wall thickness. Error bars are ± 1 s.e.

-Male

i/ Spermatozoa

The mean density of spermatozoa fluctuated less than was observed for mature oocytes **(Figure 5.16a)**. Mean relative density of spermatozoa declined gradually from 53.3% in January to a low of 38.9% in June. Density of spermatozoa remained at levels similar to those of June until October, after which the density increased to a peak of 80.2% in December. In January 1992, the spermatozoa density declined to 69.2%.

ii/ Spermatocytes

Trends in the density of spermatocytes were the converse of those for spermatozoa, retaining a lower mean relative density throughout the sampling period **(Figure 5.16a)**. An abrupt decrease in density in December to 16.8% was matched by an increase in density of spermatozoa.

iii/ Trabeculae

The density of trabeculae in male *Turbo* followed a trend similar to that shown for density of the trabeculae in females **(Figure 5.16b)**. Levels steadily increased from 4.7% in January to peak at 24.3% in June 1991, thereafter decreasing to 4.8% in October.

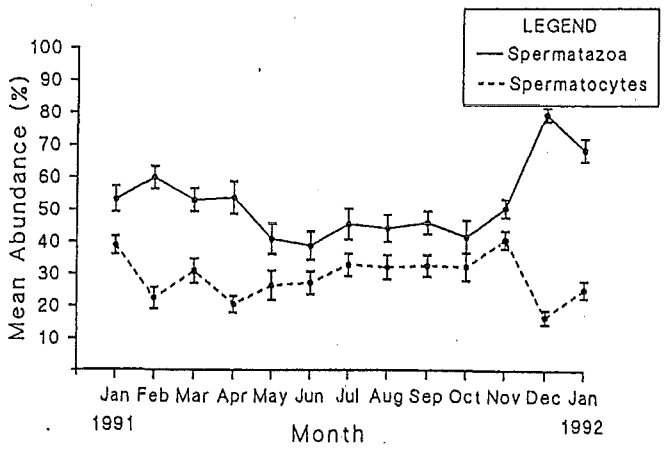
iv/ Extra-cellular matrix

Greater fluctuations occur in the density of extra-cellular matrix in males than in females **(Figure 5.16b)**. Relative density of extra-cellular matrix increased with increasing relative density of trabeculae, decreasing to 1.1% in October and 0.0% December 1991-January 1992.

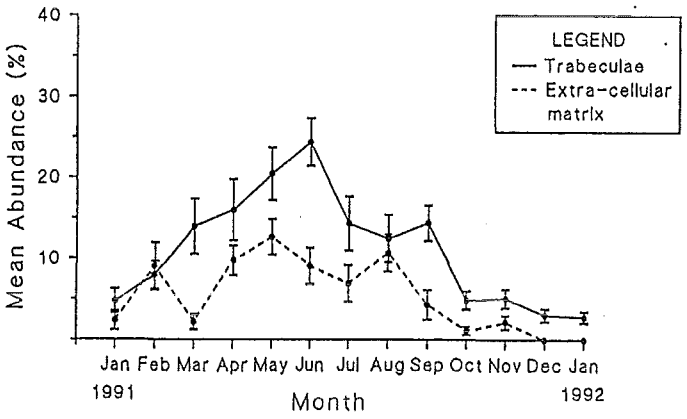
v/ Thickness of Testis Wall

The mean thickness of the testis wall was slightly greater in months of decreased spermatozoa density **(Figure 5.16c)**. Wall thickness increased gradually from 0.025mm in January, peaking at 0.054mm and 0.063mm in May and September 1991 respectively. An abrupt decline in thickness occurred in December, corresponding to a decrease in the density of spermatocytes and an increase in the density of spermatozoa. A sharp increase in wall thickness to 0.056mm in January is associated with a large standard error.

a)



b)



c)

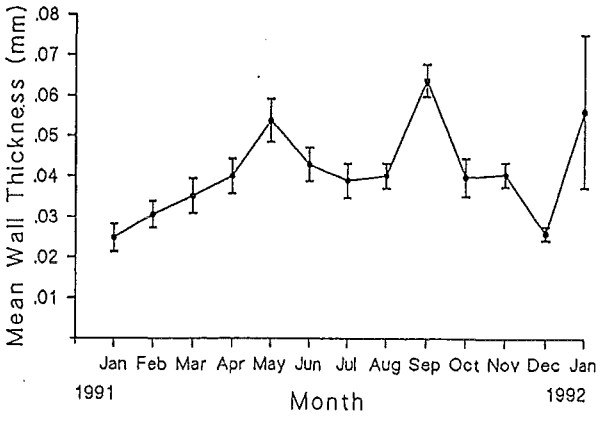


Figure 5.16 Gonad composition of male *Turbo* as described by mean monthly density between January 1991-January 1992 of **a)** spermatozoa and spermatocytes **b)** trabeculae and extra-cellular matrix **c)** mean testis wall thickness. Error bars are ± 1 s.e.

5.3.4 Fecundity

Fecundity was measured as an estimation of number of oocytes in the ovaries of female *Turbo* sampled from Lab Rocks in January 1992. This increases exponentially with increasing shell length **(Figure 5.17)**. An individual of shell length 30mm has an expected fecundity of $4.0x10^{4,}$ and at 40mm, $9.0x10^{4}$.

Individual variability in fecundity, as expressed by standard errors, also increased with increasing shell length. Mean fecundity of *Turbo* with shell lengths 25-30mm have a standard error of ±0.350, and animals of shell lengths 40-45mm, ±2.95.

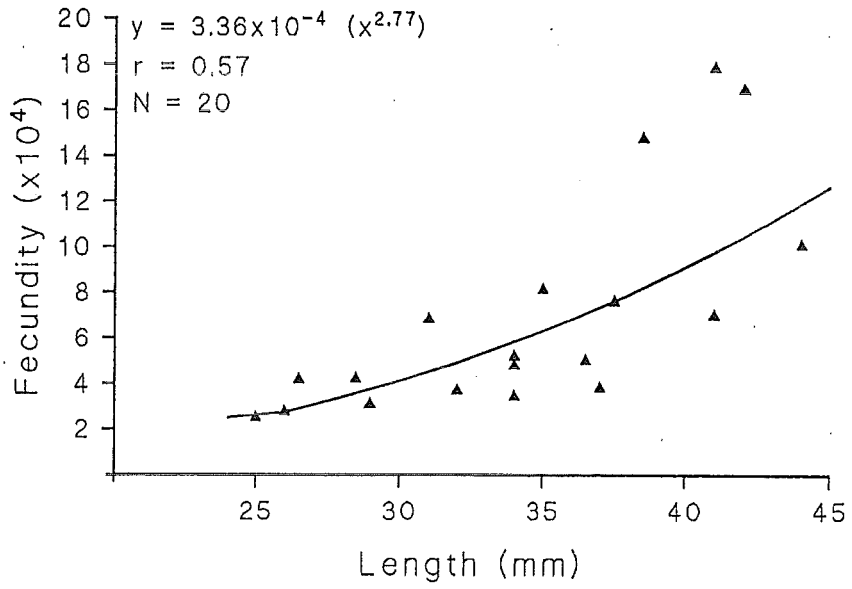


Figure 5.17 Fecundity against shell length of female *Turbo* in January 1992.

5.3.5 Sex Ratio

Of the 332 specimens randomly sampled, 167 were female and 165 were male. There was no significant difference from the expected ratio of 1:1 (χ^2=0.006, $p < 0.001$).

5.3.6 Size at Sexual Maturation

-Female

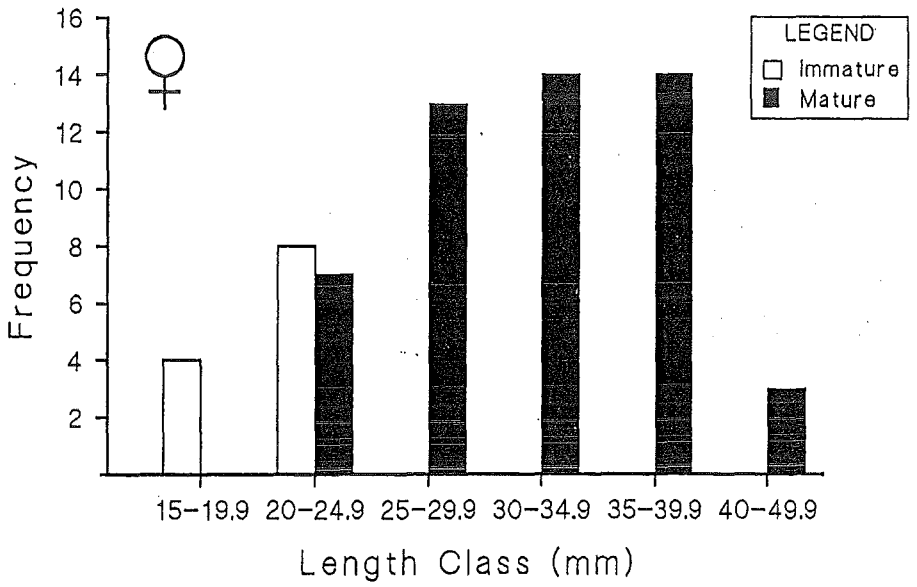
Sexual maturity of females at Lab Rocks was attained between shell lengths of 20-25mm **(Figure 5.18a)**. Of the 15 individuals examined in this size class, mature oocytes were present in the gonads of seven females. No mature oocytes occurred in *Turbo* examined in the 15-20mm size class, while all individuals examined between the 25-30mm to 40-45mm size classes were mature.

-Male

Sexual maturity of male *Turbo* at Lab Rocks was attained by the majority of individuals between shell lengths of 20-25mm **(Figure 5.18b)**. Of the nine males examined at shell lengths of 20-25mm, spermatozoa were evident in four. However, sexual maturation can occur at shell lengths of 15-20mm. All male *Turbo* of 25-30mm and greater were mature.

Immature *Turbo* of shell lengths 30-40mm were observed outside of the sampling period. The gonads of these individuals were brown and indistinguishable from the digestive gland. Neither mature nor immature gametes were observed when slides prepared from the gonads were microscopically examined.

a)



b)

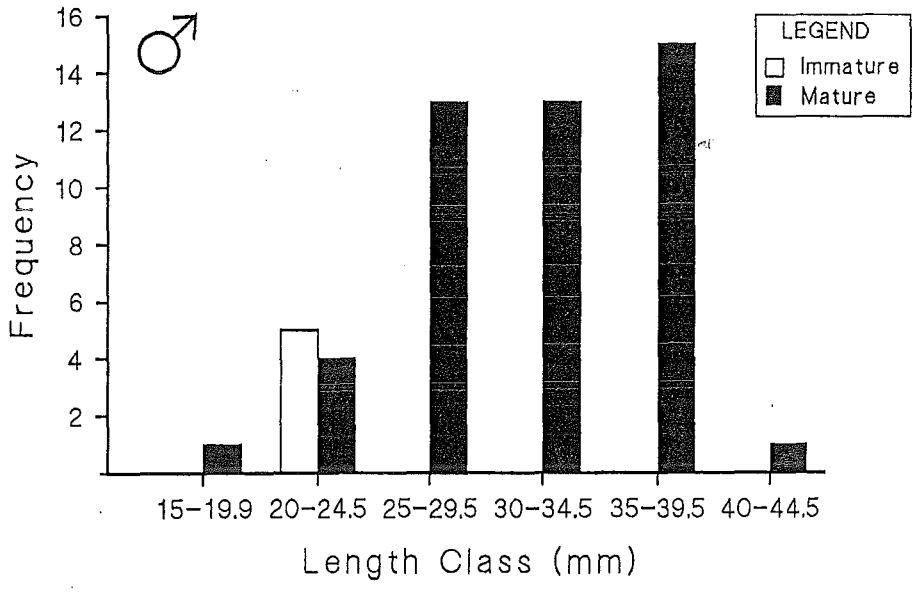


Figure 5.18 Frequency of sexually immature and mature *Turbo* sampled from Lab Rocks between October 1991-January 1992 **a)** female **b)** male.

5.4 DISCUSSION

5.4.1 Gametic Activity and Spawning Seasons

Two spawning events were evident during the 1991/1992 sampling of the *Turbo* population at Lab Rocks, Kaikoura. This corresponds to the observations of Giese (1959), that broadcast spawners generally have an annual reproductive cycle. The first spawning season occurred in February/March 1991, which was similar to that found by Grange (1974). However, the spawning season in 1992 was short and evident as an abrupt decrease in gonad indices in January, whereafter gonad indices remained high. This may be indicative of a partial spawn.

The spawning season of 1991 appeared to be a discrete, annual event which occurred in late summer/early autumn. Similarly, *Haliotis iris* also spawn at that time of the year (Poore 1972, Sainsbury 1982, Wilson 1987). Although *Turbo* are capable of releasing gametes more than once during a spawning season (Grange 1974), it is unlikely that a second spawning season could have occurred in 1991 because the gonads of both sexes were depleted of mature gametes during the first spawn and remained so for the duration of the winter.

In most broadcast spawners, the gonad enters a 'resting' phase in which gametes are absent (Orton *et al* 1956, Loosanoff 1962). However, gonad indices and number of mature oocytes of *Turbo* at Fergusson Wharf increased throughout winter (Grange 1974). At Lab Rocks, gametes were present in the gonads of both female and male *Turbo* throughout the year. Gametogenesis occurred within a month of the 1991 spawning, but oocytes only grew slowly in size (a consequence of vitellogenesis) during autumn/winter 1991. Vitellogenesis increased abruptly in the spring of 1991, as was evident from increased size of immature oocytes and density of mature gametes.

Trends in gamete development and overall gonad condition of *Turbo* at Lab Rocks varied between 1991/1992. In 1992, the density of mature gametes returned to pre-

spawn levels within a month, indicating that gametogenesis and the mid post-spawn phase that occurred in the autumn/winter 1991 did not occur in 1992.

Differences in the size of the spawning events between 1991/1992 at Lab Rocks indicate that the reproductive cycles of *Turbo* can vary annually. Similar temporal inconsistencies in annual reproductive trends have been observed for other species of gastropods. Spawning seasons can be evident as; **a)** major depletions of gametes as occurred in 1991 at Lab Rocks, **b)** short seasons, whereby gametes swiftly return to post-spawn densities as occurred in 1992 at Lab Rocks, **c)** not occurring at all (Newman 1967 as cited in Wilson 1987, Poore 1972, Underwood 1972, Underwood 1974, Sainsbury 1982).

Although not examined in this study, spawning of archaeogastropods have been observed to vary not only temporally, but spatially. Webber *et al* (1969), found that two abalone populations separated by 7 kilometres spawned 6 weeks apart. Similar observations were made by Poore (1972), Shepherd *et al* (1974) and Sainsbury (1982).

Periodicity and trends in the reproductive cycles are controlled by endogenous and exogenous factors which serve to regulate and synchronise gamete activity (Webber 1977). Endogenous controls are those that act more or less independently of external controls, such as the endocrine system. However, external factors may act on the endogenous regulating system, thereby indirectly influencing gametogenesis (Webber *et al* 1969). Exogenous controls are those acting externally to the organism, continually influencing the gonad through all stages of gametogenesis (Webber *et al* 1969). The use of endogenous cues to control reproductive cycles is advantageous in that they can act over large geographic areas. In this way, synchronisation of the reproductive activities of individuals can occur not only within and between populations, but with conditions favourable for those particular activities.

Water temperature is an exogenous factor that is thought to influence reproductive cycles in marine gastropods (Orton 1920, Thorson 1960, Giese 1959, Kinne 1963,

Smith *et al* 1967, Webber *et al* 1969). Gametic activity and gonad indices correspond to increasing water temperatures in some abalone species (Poore 1972, Wilson 1987), but not all (Webber *et al* 1969). Webber (1977) suggested that the influence of temperature depends on geographical location. For example, gametogenesis of *Haliotis cracherodii*, which occurs on a northern Pacific coast where temperature fluctuations are about 5°C, was not related to temperature (Webber *et al* 1969), but gametogenesis of *H.discus*, which occurs in Japan where water temperature has an annual seasonal fluctuation of about 15°C, was restricted to the summer (Tomita 1967 cited in Webber 1977). Gonad indices continued to increase for *Turbo* at Fergusson Wharf throughout the winter (Grange 1974), unlike that of Kaikoura, where gonad indices for both sexes did not increase until spring. This may be the result of geographic differences.

Nutrient supply may be important in affecting gametogenic development (Segal 1956, Sutherland 1970). Shepherd (1973) found that maximum gonad growth in *Haliotis laevigata* and *H. cyclobates* may coincide with that of an abundant food supply. Increasing water temperatures in spring may coincide with increasing availability of food. The rapid growth of gametes in spring that was observed at Lab Rocks and at Fergusson Wharf (Grange 1974) may, therefore, be the result of increasing availability of nutrients that are directed into gonadal development.

Orton (1920) divided marine invertebrates into those that spawned near maximum summer temperatures and those that spawned on falling or minimum temperatures. *Turbo* spawned in autumn, as does *Haliotis iris* (Poore 1972, Wilson 1987). Survivorship of settlers from the plankton may be enhanced by an autumn spawn, due to avoidance of the higher temperatures and desiccation that are associated with summer. However, declining temperatures are unlikely to serve as the exogenous cue to the onset on spawning in *Turbo*. Grange (1976) suggests that the onset of spawning at Fergusson Wharf was initiated by the vigorous water movement of storms in late summer/early autumn. Similar suggestions have been forwarded by Orton *et al* (1956), Costello *et al* (1957, cited in Grange 1974) and Pilkington (1971). Some

advantages of storms acting as the cue to the onset of spawning include: **a)** Storms are able to act over wide areas, thereby, synchronising the population and maximising numbers of gametes available for fertilisation in the water column. **b)** Increasing genetic diversity by mixing of gametes from different areas. **c)** Dispersal of larvae over a wide area.

Exogenous factors such as temperature, availability of food and storms, vary spatially and temporally. Therefore, if exogenous factors to control the reproductive cycle of *Turbo*, variations in gametic activity and spawning would be expected. Spawning events and trends in gametic activity of *Turbo* at Lab Rocks varied within and between years.

Exogenous cues can serve to synchronise gametic and reproductive activity between individuals and the sexes of a population. This is of particular importance to broadcast spawners because synchronicity increases the likelihood of successful fertilisation of gametes in the water column. Synchronization of reproductive cycles and spawning seasons was exhibited by *Turbo* at Lab Rocks. This is illustrated by similarity in gonad indices throughout the sampling period and the onset of spawning occurring in the same months for both sexes.

The variability in spawning seasons and gametic activity, as was exhibited by *Turbo* at Lab Rocks within and between annual reproductive periods, indicate that a single, or even two reproductive cycles may be inadequate to describe possible longer term trends in the natural cycles.

5.4.2 Comparison of Gonad Indices and Histological Analysis Techniques

Both gonad indices and histological analysis seek to determine trends in reproductive cycles of a population. Gonad indices show changes in overall size of the gonads relative to body size (Giese 1959). Histological analysis, as used in this study, shows changes in the gametic composition of the gonad.

Gonad indices for both sexes of *Turbo* indicated that the weight of the gonad decreased after spawning, but gradually increased throughout winter and into spring. Histological analysis indicated that the density of mature and immature gametes did not fluctuate greatly over autumn/winter. However, the density of mature gametes increased markedly during spring. From these results it can be surmised that gametogenesis occurs shortly after spawning, and that the gametes, which will remain in the gonad until release are generated over a short period after spawning. In this way, the relative density or the number of immature oocytes will not alter, but as the size of immature oocytes increases as they develop into mature oocytes in the gonad, the overall weight or volume of the gonad will increase.

The onset of gametogenesis was not indicated by plots of gonad index because the process involves negligible changes in gonad volume. However, the onset of increased rate of vitellogenesis is recorded. Gonad index techniques assume that increasing gonad weight/volume is associated with increasing number and/or size of gametes. Changing quantities of non-gametic material is not, nor can be, differentiated from changes in gametic quantity. Therefore, if detailed information of the processes and composition of the gonad throughout a reproductive cycle are required, histological analysis of gonads is required.

Gonad index techniques would be of limited value in predicting the onset of spawning events in species which do not have: **a)** synchronised reproductive trends in the majority of individuals **b)** mass release of gametes from the gonad over a short period.

The point-count method that was used in this study did not reflect the changes in volume of *Turbo* gonads throughout the reproductive cycle. Therefore, although indicating changes in overall gonad composition, measurements of gamete and extra-cellular density are 'relative'. This can be avoided if the total cross-sectional area of the gonad is used as a measure of gonad index. It is of use, in this study, to compare plots of gonad index with those of gamete density.

Gonad index methods are a quick means of acquiring basic information on the periodicity of a species'reproductive cycle. Histological techniques, although provide more detailed information, are considerably more time consuming. Both methods, as used in this study, have limitations, but when used in conjunction, a more accurate interpretation of trends can be determined.

5.4.3 Fecundity

Fecundity is greater in broadcast spawners than other non-broadcast spawning prosobranchs (Webber 1977) and can be attributed to the need to increase the probability of fertilisation of the gametes in the water column.

Fecundity of *Turbo* at Lab Rocks increased directly with increasing shell length. Similar trends occurred with fecundity of abalone (Poore 1974, Sainsbury 1982, Wilson 1987) and lobster species (Annala *et al* 1987). Although mature gametes did occur in smaller individuals, their contribution to the populations' total egg output would be negligible (Poore 1972). Therefore, although not examined in this study, contribution to overall reproductive effort is likely to increase with increasing fecundity.

Variability in fecundity between individuals increases with increasing size of *Turbo* at Lab Rocks and similarly in *Haliotis iris* (Sainsbury 1982). Likewise considerable variability of fecundity is shown to occur between localities (Sainsbury 1982).

Fecundity is an expression of an individuals' energetic investment in reproductive effort. Younger individuals' energy consumptions are expressed as growth, but with increasing age, more energy is spent on gonadal development and less on growth.

5.4.4 Sex Ratio

No significant difference was found in the sex ratio of *Turbo* at Lab Rocks. These results differ from the suggestion by Fretter *et al* (1964) that females are more

common than males in dioecious molluscs, thereby suggesting differential mortality or growth rates between the sexes. Growth rates of each sex were not determined in this study because sex cannot be evaluated externally. Some Haliotid species are known to also deviate from the conclusion of Fretter *et al* (1964) (Boolootian *et al* 1962, Shepherd *et al* 1974, Wilson 1987).

5.4.5 Size at Maturation

Mature gametes were observed in gonads of both female and male *Turbo* of shell lengths 20-25mm. Some individuals may mature at smaller sizes as occurred in one of the sampled males, but all individuals examined in this exercise were mature at 25-30mm. Using the shell length against age curve as estimated by the von Bertalanffy growth model for Whakatu Point (Chapter Three), *Turbo* of shell length 20-25mm are 3-4 years in age. The Whakatu Point curve was used to determine the size at age of maturation of *Turbo* because it was the site nearest to Lab Rocks at which growth rates had been determined.

Grange (1974) determined that at 13-14mm, 80% of males sampled were mature and at the end of 2 years when *Turbo* were 14-16mm, 50% of both sexes were mature. *Turbo* at Fergusson Wharf achieved sexual maturity at smaller shell lengths and 1-2 years earlier than those at Lab Rocks.

5.4.6 Concluding Comments.

Turbo, characterised with the primitive reproductive system common to archaeogastropods, have an annual reproductive cycle that varies considerably within and between years. Reproductive effort is seasonal and increases considerably with increasing size of individuals. Therefore, to describe trends in reproductive cycles

adequately, it is necessary to study: **a)** individuals of a wide range of sizes, **b)** more than one spatially distinct population, and **c)** cycles for at least two years.

CHAPTER SIX

GENERAL DISCUSSION

Turbo smaragdus is the most abundant herbivorous mollusc of the shores sampled on the Kaikoura Peninsula. The species has a wide distribution not only along the coastline of New Zealand (Morton and Miller 1968), but within and between sampling sites in the Kaikoura Region.

Turbo occur in areas exposed to a range of wave actions including: **a)** sheltered sites such as Lab Rocks, Kaikoura and in some mangrove areas of the North Island (Walsby and Morton 1982), **b)** sites of moderate exposure such as Spaniards Bay, and **c)** exposed sites, such as Paia Point and Haumuri Bluffs. *Turbo* are distributed from the upper eulittoral of the intertidal zone, to depths >6m in the sub-littoral zones at Spaniards Bay, although *Turbo* have been observed at greater depths both in the Kaikoura Region and in the Pelorus Sounds (Lindsay Chadderton, *pers. comm.*). The substrata on which *Turbo* were found on the Kaikoura Peninsula included: siltstone (e.g., Avoca Point, Lighthouse Reef), limestone (e.g., Spaniards Bay) and sand (e.g., some areas of Whakatu Point).

The numbers of *Turbo* encountered during sampling differed significantly between sites, transects and shore heights. The least number of *Turbo* were found on the upper shore, while greatest numbers generally occurred on the mid shore. *Turbo* have an aggregated distribution when sampled at low tide. This is supported by high numbers of quadrats in which no *Turbo* were present and a smaller number in which several or more were present.

Turbo exhibit a size-frequency gradient along the vertical profiles of the shores sampled. Smaller individuals (shell lengths 5-15mm) occurred between the upper eulittoral and sub-littoral fringe of the intertidal zone, while larger individuals (shell lengths ≥25mm) were generally confined to the lower eulittoral and sub-littoral zones.

All individuals of the sub-littoral population sampled in Spaniards Bay were of shell lengths ≥35mm, and individuals of shell lengths 50-60mm occurred in the sub-littoral populations of Paia Point.

Numbers of *Turbo* within each shore height varied between months of the year at Avoca Point and Spaniards Bay. This may be indicative of vertical and lateral movement of *Turbo* on the shore. Recruitment of *Turbo* (shell lengths <5mm) was not observed at either of the two sites in 1991/1992. This may indicate of: **a)** the failure of the breeding stock spawned, **b)** failure of the planktotrophic larvae to arrive at those sites **c)** early mortality of the settlers on the shore or **d)** failure of the animals to be detected in the sampling. Considering: **a)** the absence of recruits in April 1992 (even when searched for microscopically) and, **b)** knowing that spawning events vary between years (as indicated in Chapter Five, Reproduction), it seems likely the breeding stock, (which may be different from the Lab Rock population that was sampled) that supplies Spaniards Bay and Avoca Point with larvae failed to spawn.

Turbo were not strongly associated with other herbivorous molluscs, algal species or substratum types on the shores sampled. This may reflect the gentle slope of the shore which possibly results in a gradual gradient of the physical factors that are thought to influence the zonation of organisms on the shore (Morton and Miller 1968). However, the absence of strong correlations with the flora, fauna and substratum types of the shore is also indicative of the species' ability to survive in a broad range of habitats, not only along the vertical profile of the shore, but between sites and along the coastline of New Zealand.

The various measures of *Turbo*'s shell and body dimensions are highly correlated (all $r^2 \geq 0.97$). This is useful because the measurement of an external dimension of an individual, such as shell length, can used to estimate with reasonable accuracy dimensions that may not be as easily measured in the field (such as body weight).

Significant variability of the growth rates occurred between: **a)** individuals of a

population, **b)** seasons and **c)** sites. Growth rates decreased with increasing shell length of *Turbo*. For example, at Spaniards Bay, an individual with an initial shell length of 10mm grew 6.7mm per annum 1991/1992, while during the sample period, a 30mm individual grew 1.6mm. In length-frequency histograms the trend of decreasing growth with increasing size of *Turbo* is evident as the coalescence of age classes (modes) and in tag-release data, as the negative gradient of linear regressions that were fitted to growth increment/initial size plots.

Growth rates were greatest between November-March which coincides with warmer water temperatures and possibly increased availability of food on the shore. Insignificant growth of shell lengths occurred over the winter sampling periods.

Growth rates of Spaniards Bay were greater than those of Whakatu Point. Variability of growth rates is likely to occur because of: **a)** variability between individuals, and **b)** variability of external environmental factors that influence the *Turbo*, such as exposure to wave action (Shepherd *et al* 1974) and food availability (Shepherd *et al* 1983).

Numbers of *Turbo* recovered after one year in tag-recapture studies provide a minimum survivorship of 6% and 16% for the Spaniards bay and Whakatu Point populations respectively. Mortality estimates for these populations using this tag-recapture data are likely to be overestimated considering the initial problem of tag loss.

Sexual maturation was attained in both sexes by the majority of individuals at shell lengths between 20-25mm. However, several individuals were sexually immature at 30-35mm and one male was sexually mature at 15-20mm. Reproductive effort, as indicated by fecundity, increases exponentially with increasing shell length of *Turbo*, although there is considerable variability between individuals ($r^2 = 0.57$). In January 1992, a *Turbo* with a shell length of 25mm had a fecundity of 2.5×10^4 oocytes and a 40mm animal, 9.2×10^4 oocytes. The population exhibits a sex ratio of 1:1.

Turbo have a distinct annual reproductive cycle. Spawning events occur in late summer/early autumn, although the magnitude varies between years. A major

spawning event occurred in February 1991, after which the gonads of both male and female *Turbo* were reduced in volume and relatively depleted of mature gametes. Gametogenesis occurred within several months of the spawning season, after which the abundance and size of gametes increased throughout the winter. Growth of the gametes increased rapidly from August-November to produce gonads that were densely packed with mature gametes. In contrast, the spawning event of 1992 was minor, as evidenced by the abrupt decrease in the gonad indices of both sexes in January which returned to pre-spawn levels in February.

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APPENDIX I

a) Classification of *Turbo smaragdus*.

Phylum	Mollusca
Class	Gastropoda
Subclass	Prosobranchia
Order	Archaeogastropoda
Superfamily	Trochacea
Family	Turbinidae
Genus	Turbo
Species	smaragdus

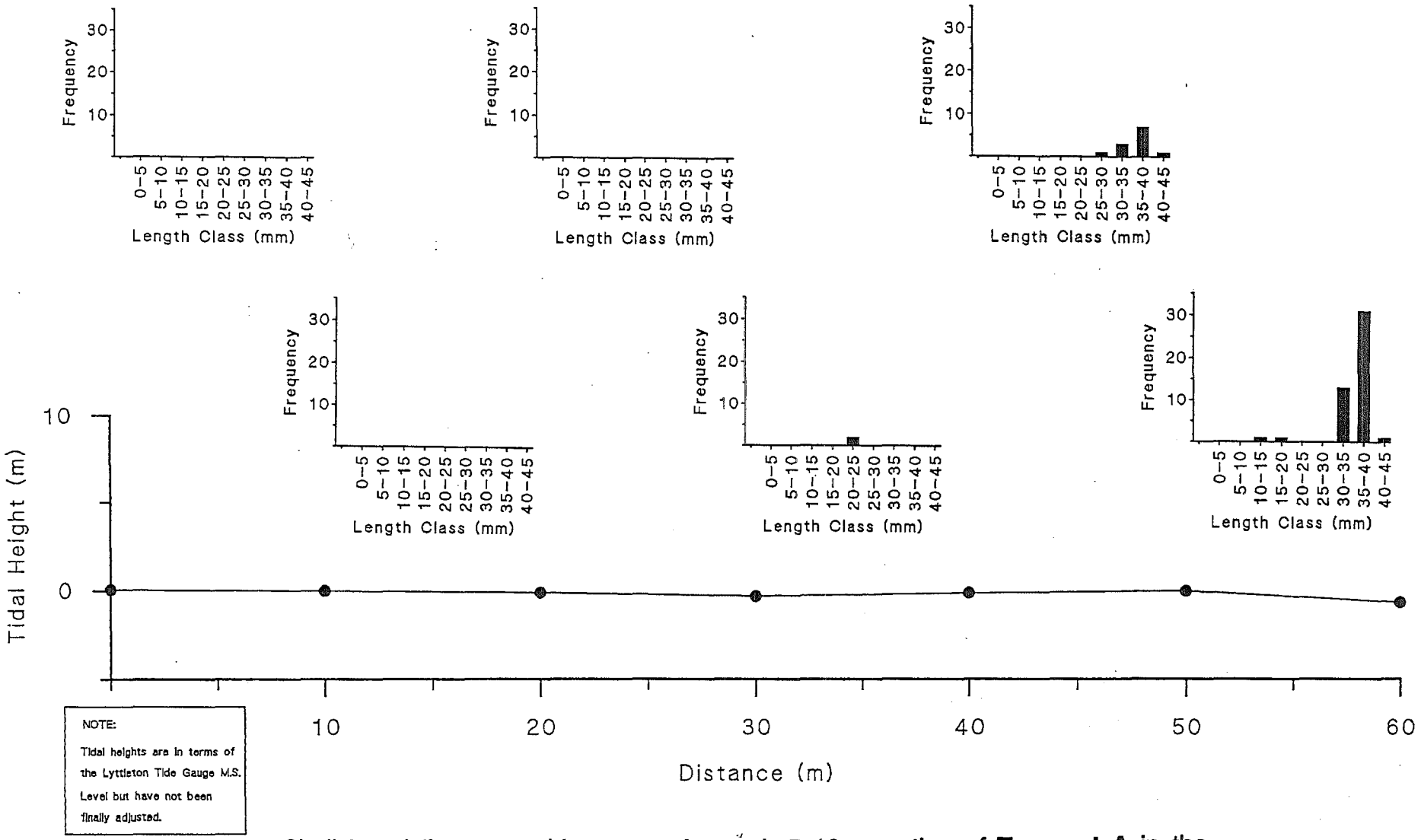
b) Other New Zealand species of the Turbinidae family. (Tabulated).

SPECIES	DISTRIBUTION
Turbo granosus	Throughout NZ. Lower eulittoral into sublittoral. Not common.
Cookia sulcata	Throughout NZ. Sublittoral. Often encountered when diving.
Astraea heliotropium	Throughout NZ. Sublittoral to 100m.
Homalopoma fluctuata	Throughout NZ. Sublittoral and mid-tide pools. Small. Rare.

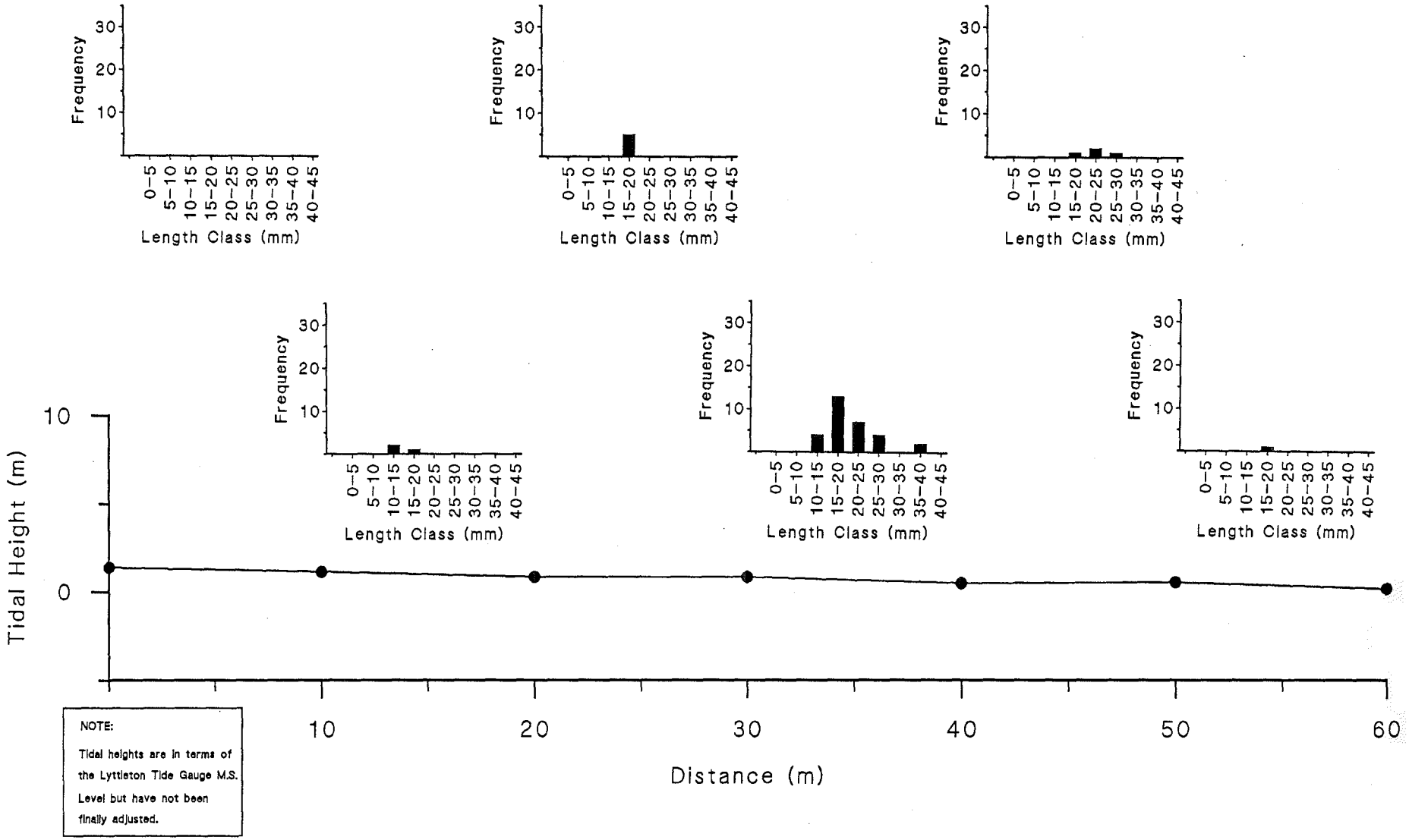
(Walsby and Morton, 1982)

APPENDIX II

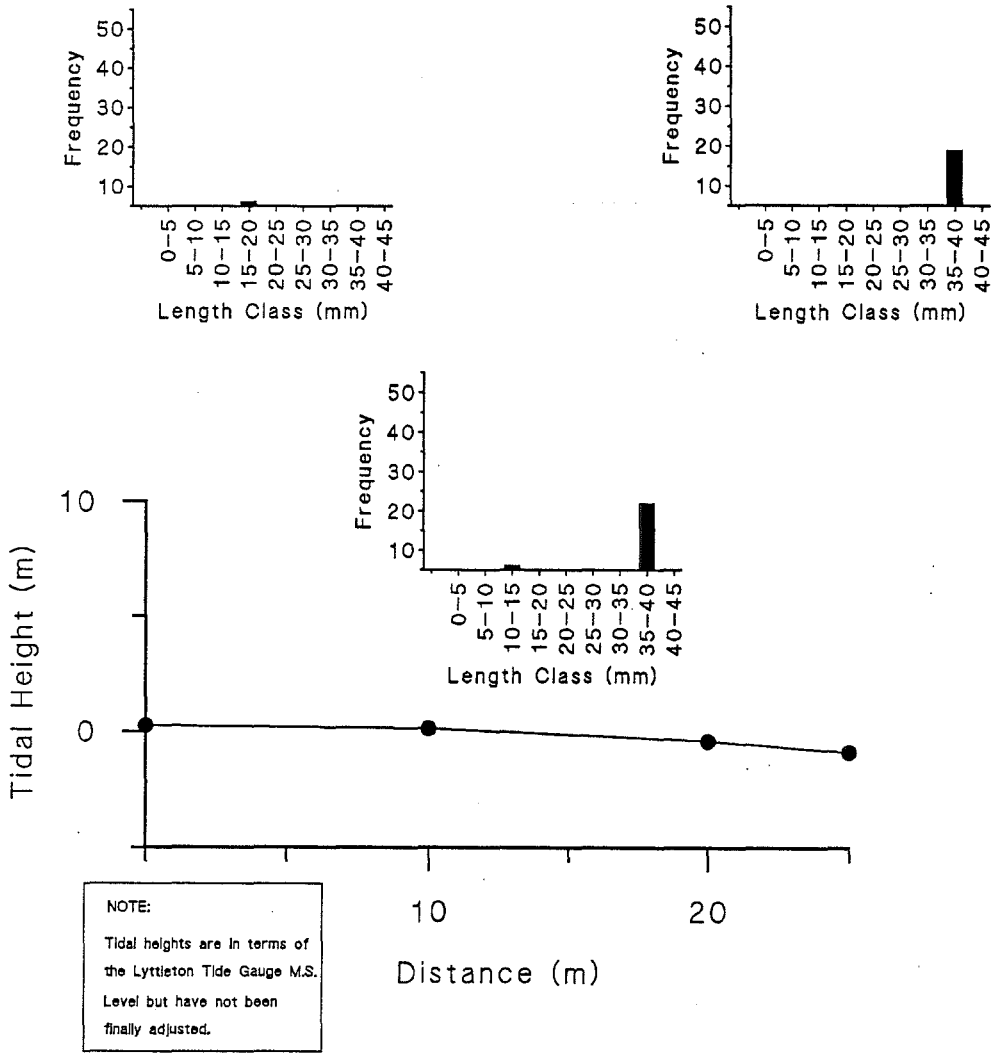
Shell/length frequency histograms for each 5x10m section of transects sampled at Spaniards Bay, Whakatu Point and Lighthouse Reef on the Kaikoura Peninsula, January 1992.



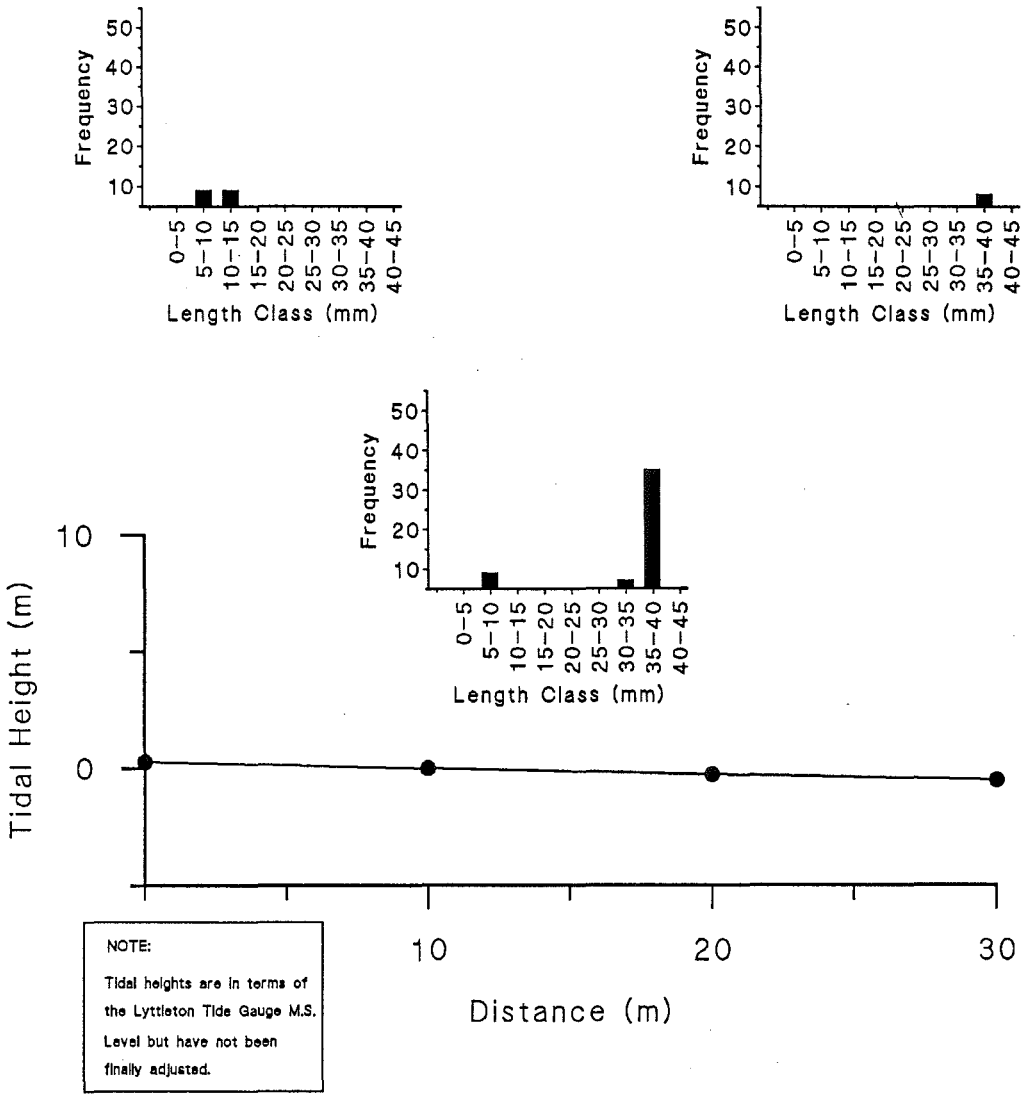
Shell length/frequency histograms for each 5x10m section of **Transect A** in the intertidal zone of **Spaniards Bay**.



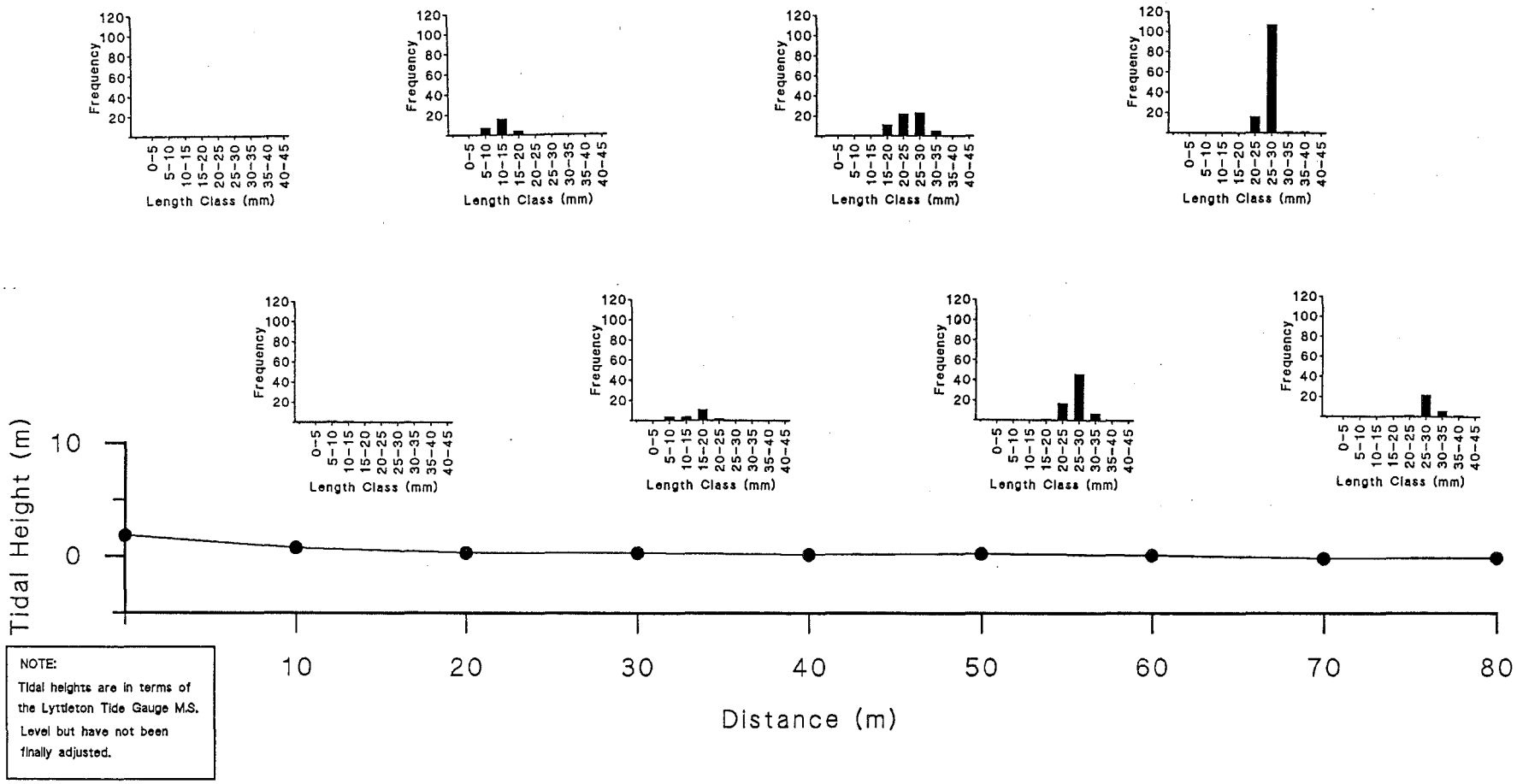
Shell length/frequency histograms for each 5x10m section of **Transect C** in the intertidal of **Spaniards Bay**.



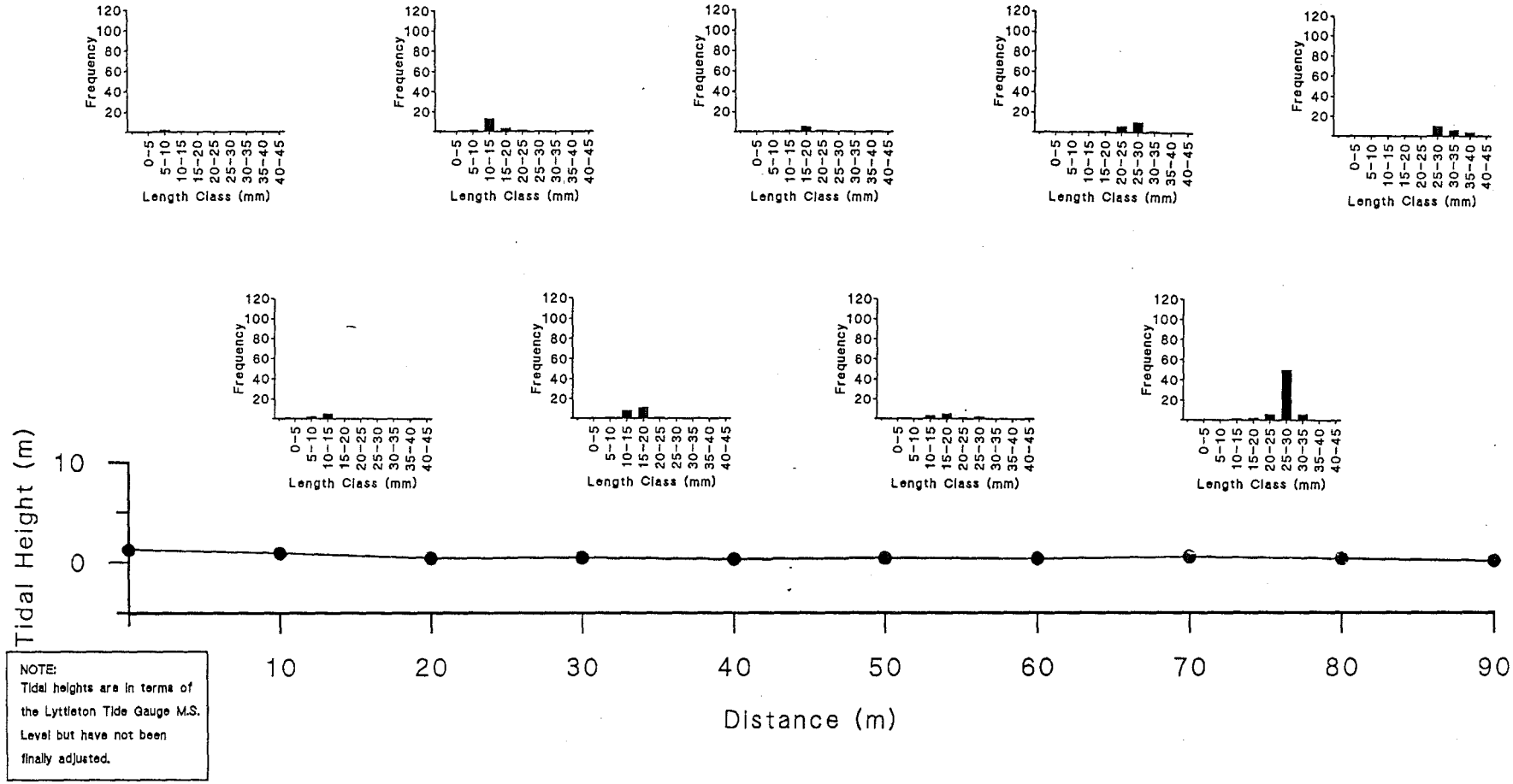
Shell length/frequency histograms for each 5x10m section of **Transect A** in the intertidal zone of **Whakatu Point**.



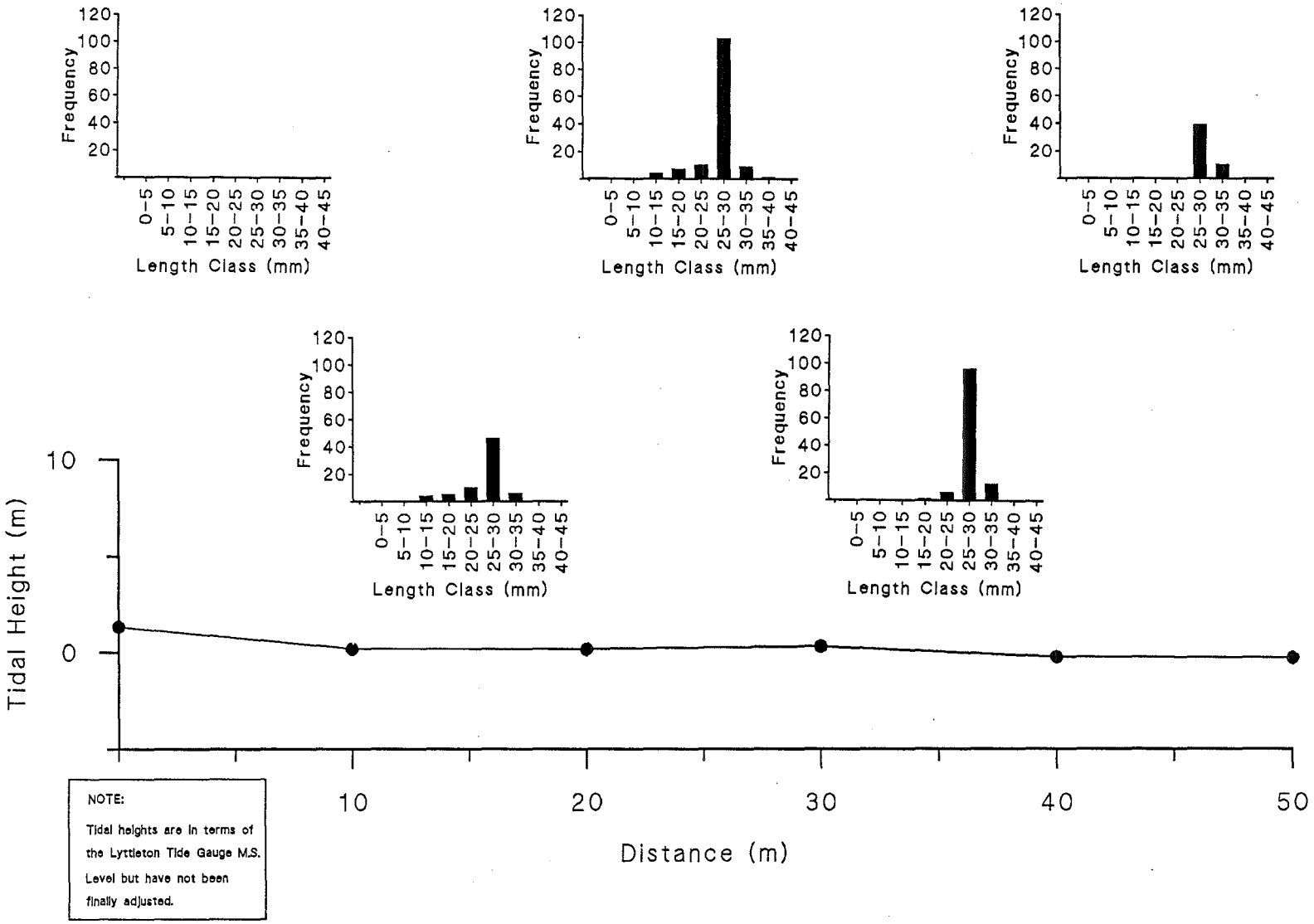
Shell length/frequency histograms for each 5x10m section of **Transect B** in the intertidal zone of **Whakatu Point**.



Shell length/frequency histograms for each 5x10m section of **Transect A** in the intertidal zone of **Lighthouse Reef**.



Shell length/frequency histograms for each 5x10m section of **Transect B** in the intertidal zone of **Lighthouse Reef**.



Shell length/frequency histograms for each 5x10m section of **Transect C** in the intertidal of **Lighthouse Reef.**

APPENDIX III

List of gastropod and algal species encountered during quadrat sampling on the Kaikoura Peninsula between 1990-1992.

FAUNA

Neogastropoda

Cominella maculosa
Cominella glandiformis
Buccinulum vittatum
Haustrum haustorium
Lepsiella scobina

Patellidae

Cellana radians
Cellana denticulata
Cellana flava
Cellana ornata

Acmaeidae

Notoacmea daedala
Notoacmea helmsi

Siphonariidae

Siphonaria zelandica
Siphonaria cookiana

Onchidiidae

Onchidella nigricans

Littorinidae

Littorina unifasciata
Littorina cincta
Risellopsis varia

Potamididae

Zeacumantus subcarinatus

Trochidae

Melagraphia aethiops
Diloma nigerrima
Diloma zelandica

Turbinidae

Turbo smaragdus
Cookia sulcata

Haliotidae

Haliotis iris
Haliotis australis

Fissurellidae

Scutus breviculus

Chitonidae

Sypharochiton pelliserpentis
Amaurochiton glaucus
Cryptoconchus porosus
Ischnochiton maorianus

FLORA

Carpophyllum maschalocarpum
Carpophyllum flexuosum
Cystophora torulosa
Cystophora scalaris
Cystophora retroflexa
Ecklonia radiata
Sargassum sinclairii
Lessonia variegata
Macrocystis pyrifera
Durvillea antarctica
Durvillea willana
Landsburgia quercifolia
Marginariella boryana

Glossophora kunthii
Adenocystis utricularis
Colpomenia peregrina
Hormosira banksii
Scytosiphon lomentaria

Ulva sp.
Zostera

Ralphsia verrucosa

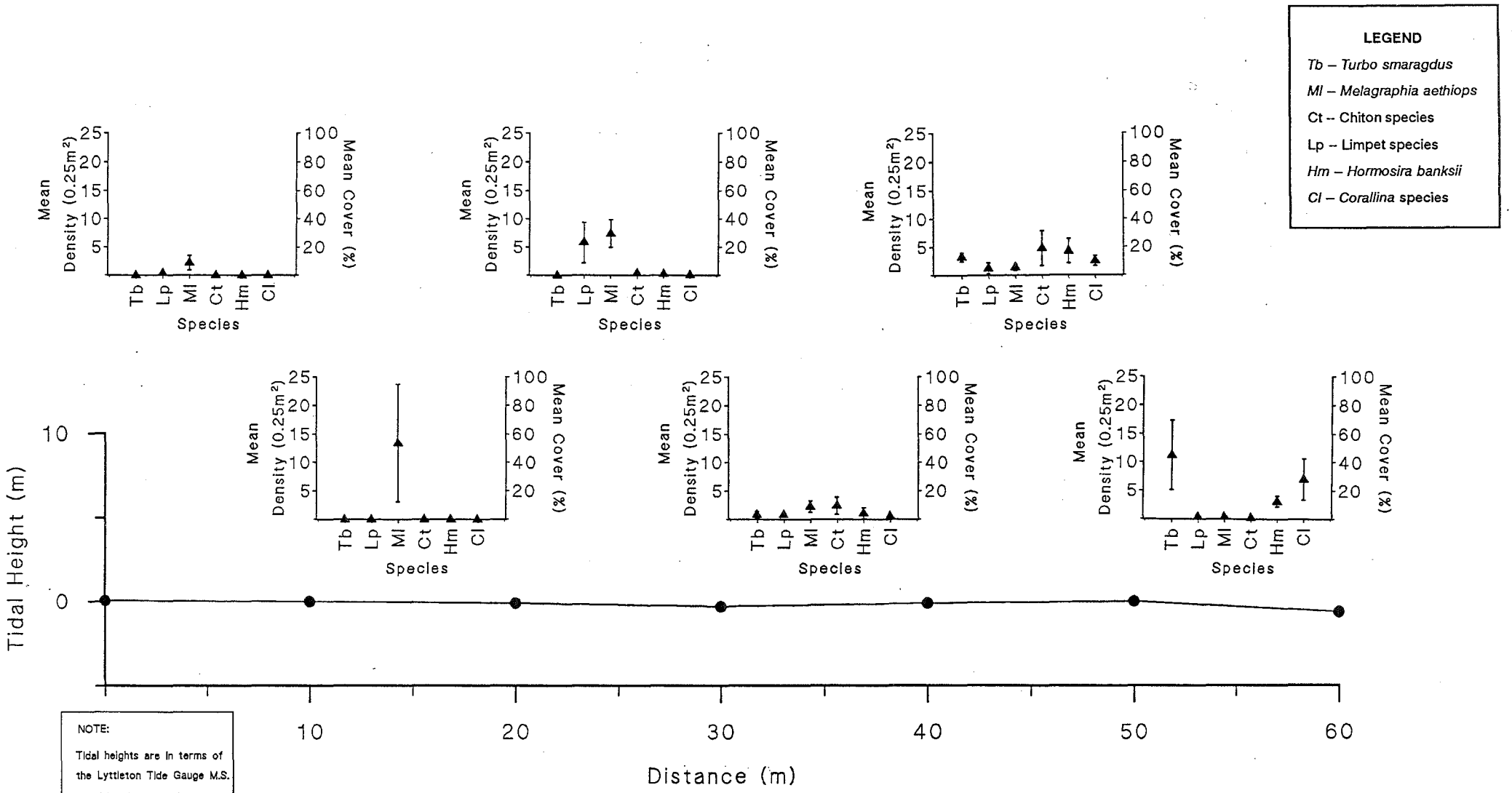
Porphyra sp.
Halopteris sp.

Corallina officinalis

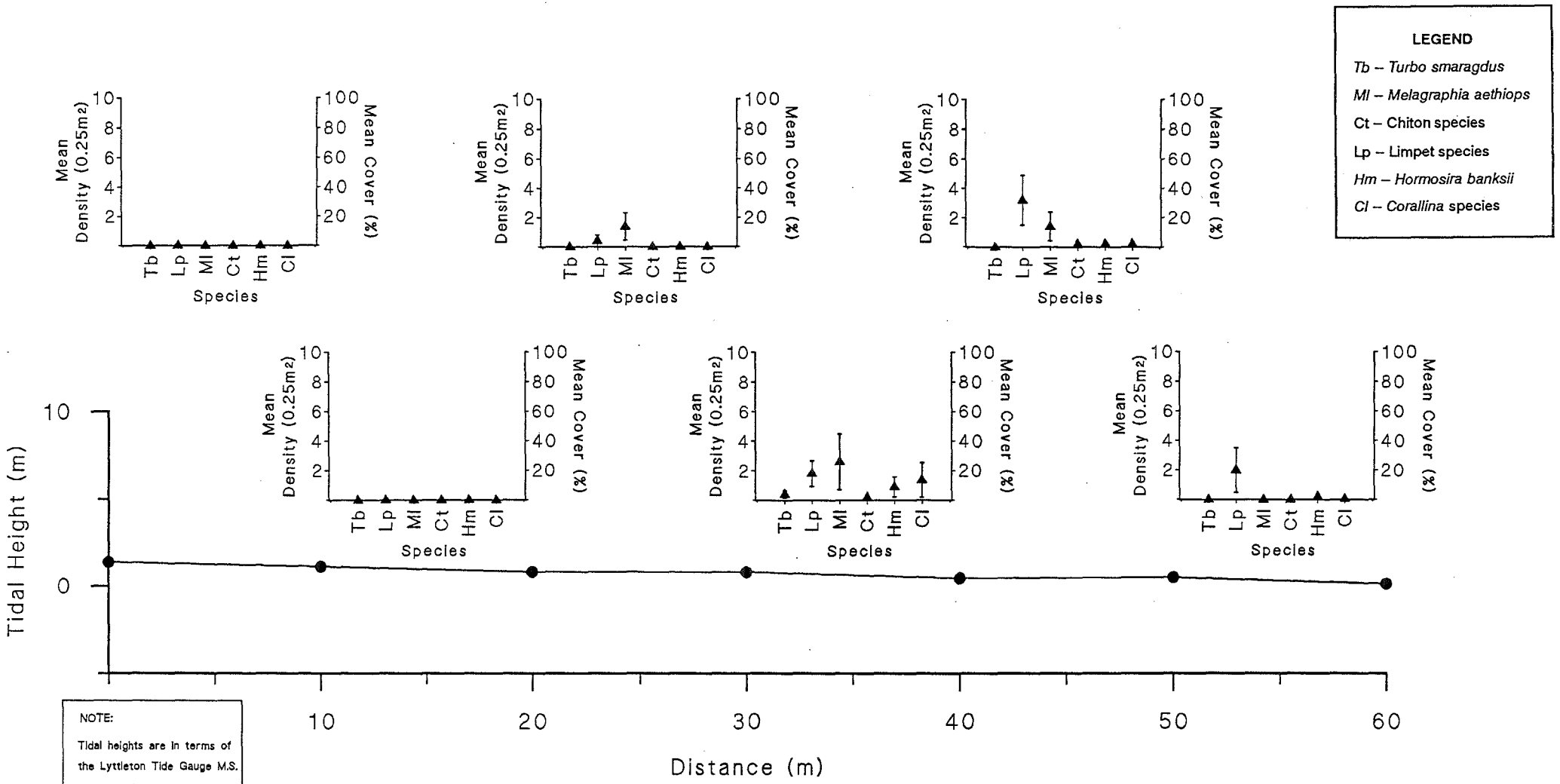
Codium fragile

APPENDIX IV

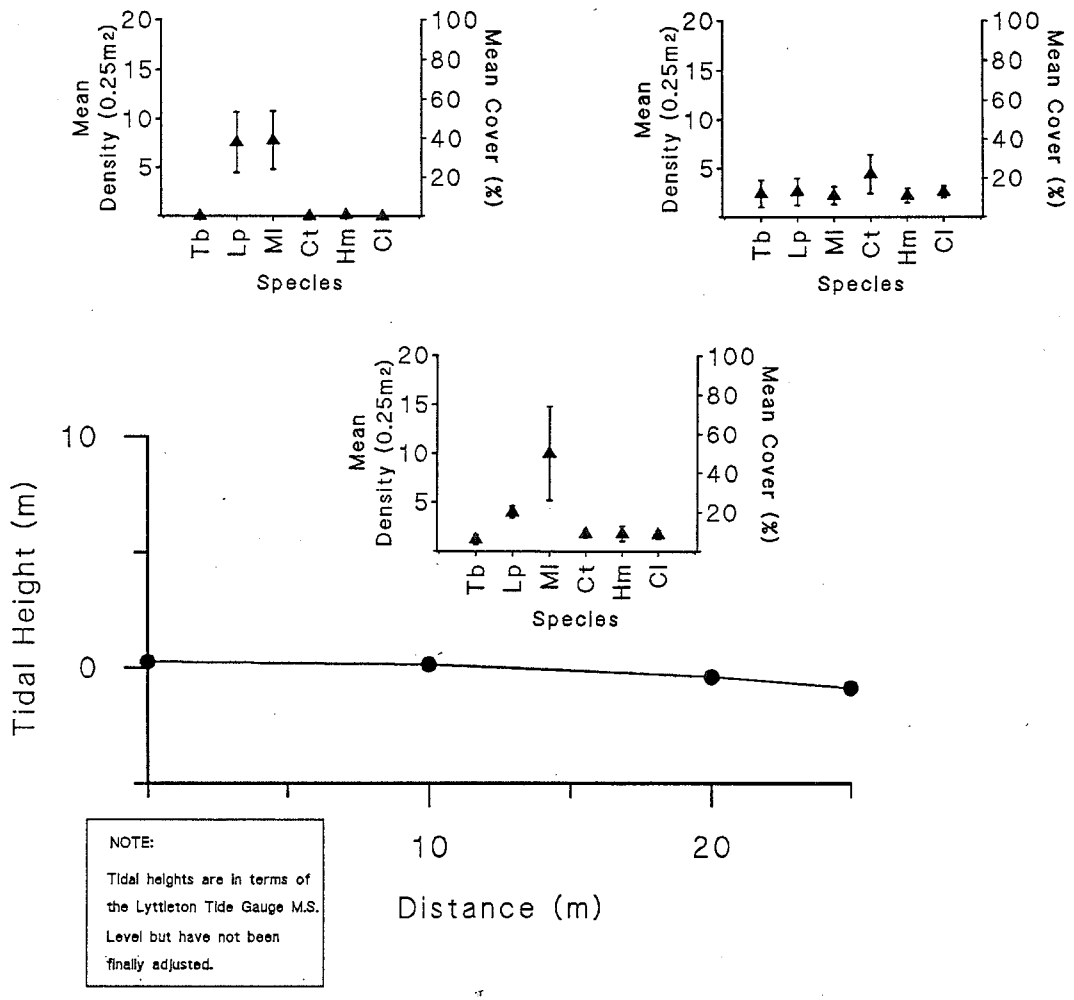
Mean densities of herbivorous molluscan species and percentage cover of algal species for each 5x10m section of transects sampled at Spaniards Bay and Whakatu Point on the Kaikoura Peninsula, January 1991.



Mean densities of herbivorous molluscan species and percentage cover of algal species for each 5x10m section of **Transect A, Spaniards Bay** in January 1991. Error bars are ±1 s.e.



Mean densities of herbivorous molluscan species and percentage cover of algal species for each 5x10m section of **Transect C, Spaniards Bay** in January 1991. Error bars are ±1 s.e.



LEGEND

Tb – Turbo smaragdus

Ml – Melagraphia aethiops

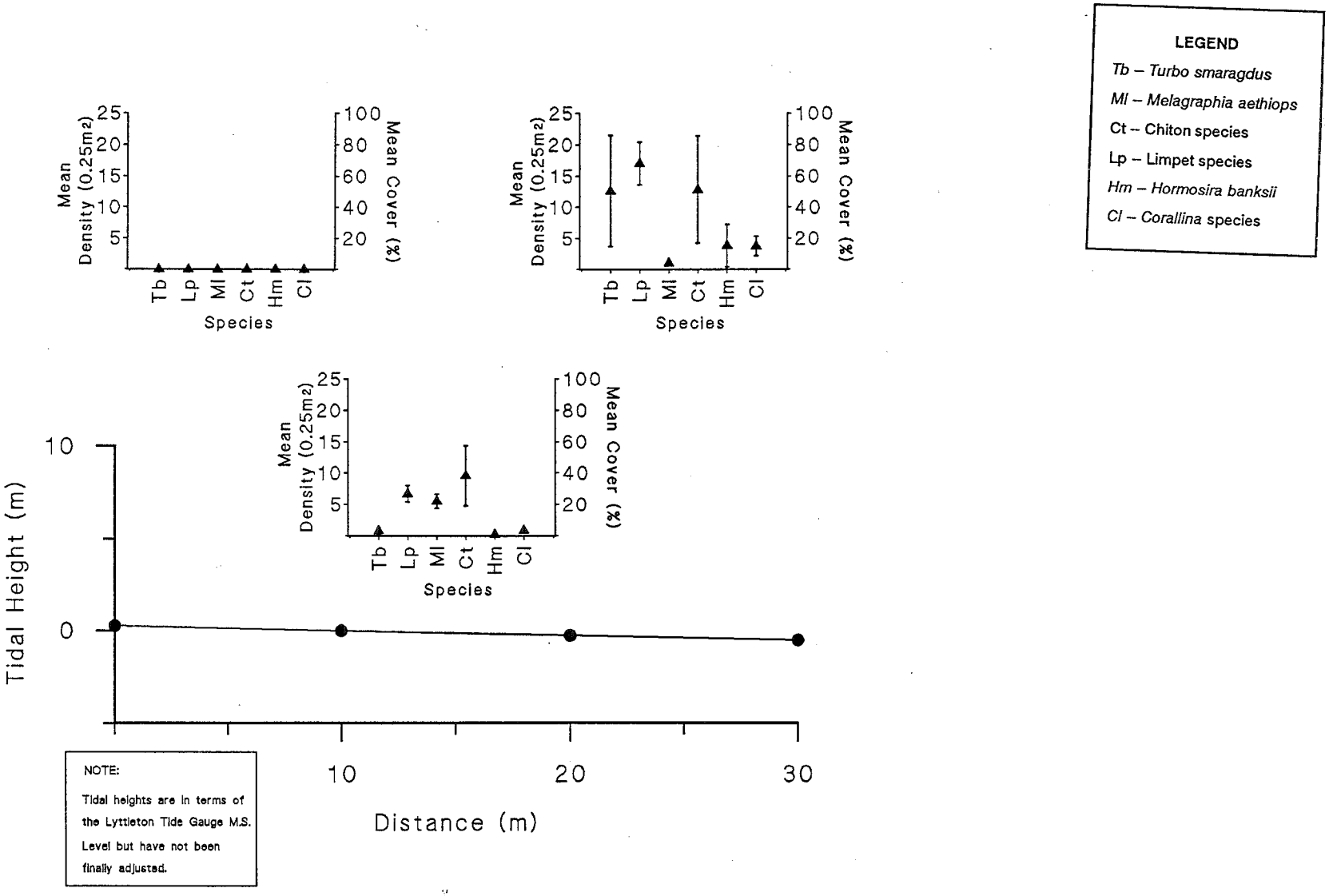
Ct – Chiton species

Lp – Limpet species

Hm – Hormosira banksii

Cl – Corallina species

Mean densities of herbivorous molluscan species and percentage cover of algal species for each 5x10m section of **Transect A, Whakatu Point** in January 1991. Error bars are ±1 s.e.



Mean densities of herbivorous molluscan species and percentage cover of algal species for each 5x10m section of **Transect B, Whakatu Point** in January 1991. Error bars are ±1 s.e.

APPENDIX V

Methods used for histological preparation of *Turbo* gonad sections.

A Tissue tek VIP 2000 vacuum infiltration processor embedded samples in an overnight cycle of approximately 16 hours, exposing them to 70% alcohol (2x), 95% alcohol (2x), 100% alcohol (4x), xylol (2x) and molten paraffin wax (2x). Samples were orientated and blocked using a Tissue Tck III Embedding Centre. Sections of embedded samples were cut at 5u on a rotary microtome using disposable razor knives, slides dried in a 60°C oven, and stained using haematoxylin and eosin.

Staining procedure involved dewaxing and hydration of slides in xylol and graded alcohols and washing in water. Slides were left in Ehrlich's haematoxylin for 15 minutes, excess dye rinsed off and dipped 15 times in 3% acid alcohol. To blue, slides were placed in Scotts tap Water Substitute and rewashed in water for 10 minutes, 1% aqueous eosin for 2 minutes and a final rinse in water before dehydrated and cleared in the series of graded alcohols and xylol. Slides were mounted with synthetic resin and a coverslip placed.